

Appendix I

Montane and Subalpine Terrestrial Ecosystems of the Southern Colorado Plateau – Literature Review and Conceptual Models

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Note: These conceptual models were prepared for the Southern Colorado Plateau Inventory and Monitoring Network and included as Supplement 1 of their Phase 2 report for Vital Signs Monitoring. They are adopted by NCPN, and included here for reference, because of their broad applicability to montane and subalpine systems of the Colorado Plateau.

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Overview

This report was prepared for the National Park Service's (NPS) Southern Colorado Plateau Inventory & Monitoring Network (SCPN), a cluster of 19 NPS units encompassing 11,892 km² in northern Arizona, northwestern New Mexico, southwestern Colorado, and south-eastern Utah. All of the units are on the southern Colorado Plateau, except for the eastern-most units in New Mexico. Of the 19 SCPN units, the following have montane/subalpine ecosystems: BAND, CACH, ELMA, GLCA, GRCA, MEVE, NAVA, SUCR, and WACA.

Ecosystems

Ecological study of the montane and subalpine ecosystems of the Southwest began in the southern Colorado Plateau in 1889 with Clinton Hart Merriam's classic research on life zones (Brown et al. 1994). Merriam's first publication on this topic, "Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona" (Merriam and Stejneger 1890), established the life zone concept, the general principles of which continue to be used in North American ecology and biogeography.

Classification

Although the ecosystem classification used in this report bears striking similarities to Merriam's classification of life zones, the recent, more direct roots of the ecosystem classification are in a series of publications by David E. Brown and usually coauthored by Charles H. Lowe and Charles P. Pase (e.g., Brown et al. 1980, Brown 1994b).

Spence et al. (1995) revised the Brown-Lowe-Pase classification system specifically for the Colorado Plateau, and this report uses a modified form of their classification of formations. For their Montane Zone (1,900-3,100 m elevation), this report includes only their Forest, Tall-Shrub, and Grassland Formations (containing ecosystems herein designated as Ponderosa Pine Forest, Mixed Conifer Forest, Montane Shrubland, and Montane Grassland). For their Subalpine Zone (2,750-3,600 m), this report includes only the Forest and Grassland formations (Spruce-Fir Forest and Subalpine Grassland Ecosystems). Ecosystems representing the other montane and subalpine formations listed by Spence et al. (1995) are not included in this report for one or more of the following reasons: (a) they are uncommon in SCPN, (b) they typically represent synusia (layers) within ecosystems rather than whole ecosystems, or (c) they are aquatic ecosystems outside the scope of this report. Also, because there is little literature clearly differentiating between the Montane and Subalpine Grassland Ecosystems, these two ecosystems are combined. The classification used here is as follows:

Ponderosa Pine Forest
Mixed Conifer Forest
Spruce-Fir Forest
Montane Shrubland
Montane-Subalpine Grassland

Although some classifications treat stands of quaking aspen (*Populus tremuloides*) as a separate forest ecosystem, this report joins Spence et al. (1995), Brown (1994b), and many others in describing and modeling quaking aspen stands as early-successional stages of coniferous forest ecosystems.

Distribution

Although this report on the montane and subalpine ecosystems of the southern Colorado Plateau recognizes the above six ecosystems, typically most of these ecosystems are better considered as sections of gradients rather than discrete ecosystems. In other words, transitions between ecosystems are generally broad, rather than narrow.

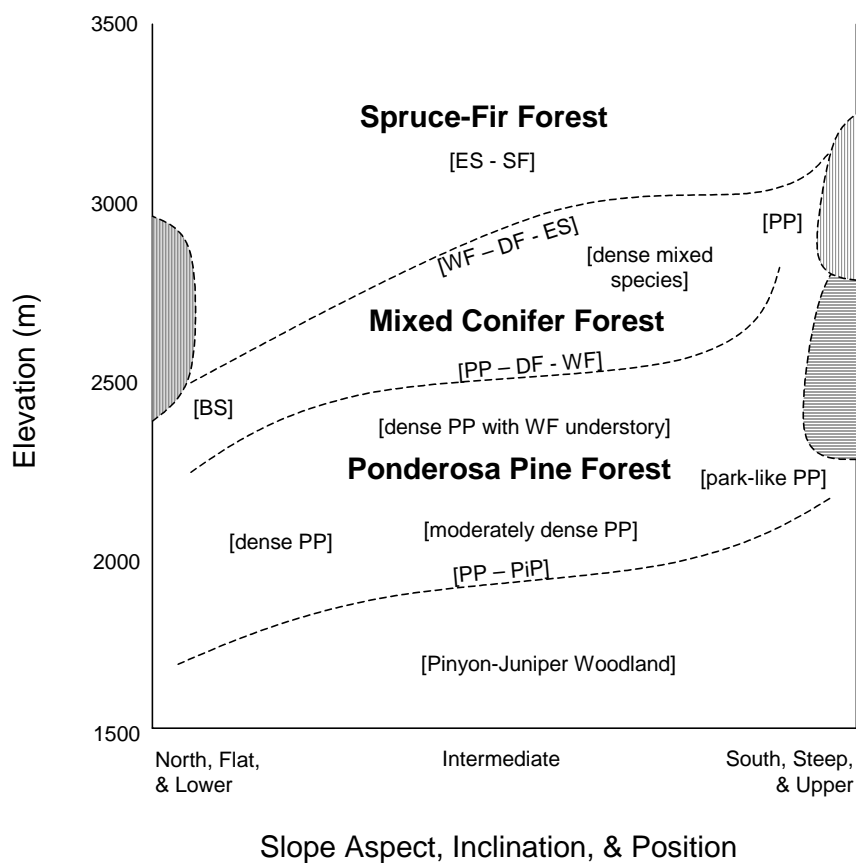
Typically, the Ponderosa Pine Forest, dominated by its namesake species (*Pinus ponderosa* var. *scopulorum*), occupies the lowest elevation of the montane zone (Figure 1). At that elevation it contains elements of the Pinyon-Juniper Woodland Ecosystem, which occurs downslope in the foothill zone. Occasionally, however, a Montane Shrubland dominated by gambel oak (*Quercus gambelii*) and other species such as mountain mahogany (*Cercocarpus montanus*, *C. ledifolius*) or serviceberry (*Amelanchier*

utahensis) occurs between the Pinyon-Juniper Woodland and Ponderosa Pine Forest.

At higher elevations of the montane zone, the Ponderosa Pine Forest becomes more homogeneous before it intergrades with the Mixed Conifer Forest. The Mixed Conifer Forest is dominated by various combinations of ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), and sometimes other species. It typically consists of a heterogeneous mosaic of patches, some of which are dominated by quaking aspen. Typically, aspen stands occur in areas relatively recently impacted by disturbance that removed the tree canopy. Scattered in the mid and high portions of the montane zone are stands of the Montane Grassland Ecosystem (in general, small stands are called meadows and larger stands are referred to as parks).

At higher elevations, the transition from the montane to subalpine zone is marked by a gradual, often patchy transition from landscape dominance by Mixed Conifer Forest to dominance by the Spruce-Fir Forest Ecosystem. The Spruce-Fir Forest is characterized by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). As in the montane zone, stands of quaking aspen may be present in sites of past disturbance, particularly in the lower elevations of the subalpine zone. Also, meadows and parks of the Subalpine Grassland Ecosystem are interspersed within the Spruce-Fir Forest.

Figure 1. Distribution of montane and subalpine ecosystems by gradients in elevation and topography. Dominant tree species for specific sites are listed within brackets (acronyms are BS = blue spruce, DF = Douglas fir, ES = Engelmann spruce, PiP = pinyon pine, PP = ponderosa pine, SF = subalpine fir, and WF = white fir)



Other ecosystems occasionally present
in place of forests on sites indicated:

Montane-Subalpine Grassland 
Montane Shrubland 

Significance

The montane and subalpine ecosystems of SCPN have regional, national, and international significance based in economic, ecologic, and aesthetic factors.

Economically, high-elevation SCPN ecosystems are significant primarily because of recreational use, with visitor use numbering in the millions. People from around the world visit SCPN units for camping, hiking, and especially sight-seeing. In the summer, the cooler temperatures of the montane and subalpine zones provide a respite from the hot temperatures that characterize much of the Southwest. In addition to recreation, the high-elevation SCPN ecosystems are economically important as watersheds, particular the subalpine zone with its deep snowpack (Moir 1993).

Ecologically, the montane and subalpine ecosystems of SCPN are important as protected examples of ecosystems that have historically been over-utilized in other areas of the Southwest. GRCA, for example, reportedly has the largest area of unharvested forest in Arizona (Fulé et al. 2002a), perhaps in the entire Southwest. Being less disturbed, ecosystems within SCPN provide some of the best of the few-remaining examples of near-natural reference conditions for scientific research and for models of management. Moreover, units of SCPN contain examples of montane and subalpine ecosystems that are uncommon outside the units. For example, GRCA has a substantial percentage of the Spruce-Fir Forest Ecosystem present in Arizona. In addition, the montane and subalpine ecosystems found in SCPN represent a great richness of biodiversity, at scales from landscapes to species. UNESCO recognized the multi-dimensional components of the ecological (and cultural) significance of SCPN units when it designated GRCA and MEVE as two of the first six World Heritage Sites in the United States.

Aesthetically, the montane and subalpine ecosystems of SCPN occur in some of the world's most spectacular landscapes. In addition to bordering sites such as the Grand Canyon, the ecosystems themselves are highly attractive, particular the meadows and parks scattered through the forests and the colorful fall foliage of quaking aspen in the Mixed Conifer and Spruce-Fir Forests. The aesthetic beauty of the montane and subalpine ecosystems was well-expressed well over a century ago by Dutton (1882) who traveled the Kaibab Plateau in and north of GRCA:

It is difficult to say precisely wherein the charm of the sylvan scenery of the Kaibab consists. We, who through successive summers have wandered through its forests and parks, have come to regard it as the most enchanting region it has ever been our privilege to visit. Surely there is no lack of beautiful or grand forest scenery in America, and it is a matter of taste what species of trees are the most pleasing. Probably few people would select the conifers and poplars [quaking aspen] as the highest types of arboreal beauty. I suspect the charm consists in influences far more subtle than these outward forms. The delicious climate, neither cold nor hot, neither wet nor excessively dries, but always exhilarating, is a fundamental condition by virtue of which the body and mind are brought into the most susceptible mood. The ease with which we move from place to place, the absence of all anxiety or care for the three great requisites of camp life, fuel, water, and grass, are accessory conditions. The contrast of the desert with its fatigue, its numberless discomforts and privations, is still another. The trees are large and noble in aspect and stand widely apart, except in the highest parts of the plateau where the spruce predominate. Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade. The ground is unobstructed and inviting. There is a constant succession of parks and glades -- dreamy avenues of grass and flowers winding between sylvan walls, or spreading out in broad open meadows. From June until September there is a display of wild flowers which is quite beyond description. The valley sides and platforms above are resplendent with dense masses of scarlet, white, purple, and yellow.

And if he had seen the other seasons...

Ecosystem Constraints and Drivers

The key characteristic of the physical setting of the montane and subalpine zones of the southern Colorado Plateau is heterogeneity -- heterogeneity in topography, climate, soil, disturbance, and

vegetation dynamics. This section provides an introduction to that heterogeneity; more detail is included in the sections on individual ecosystems.

Topography

The Colorado Plateau is a well-defined physiographic region of about 337,000 km². It is bounded primarily by the Rocky Mountains to the north and east and by the Basin and Range physiographic region to the southeast, south, and west. The Continental Divide crosses the Plateau.

Much of the Colorado Plateau consists of horizontal, relatively undeformed sequences of sedimentary and volcanic rock (Hawley 1986), but many areas have volcanic elements and deeply cut drainage systems. Common landforms include tablelands such as plateaus, mesas, buttes, and benches, as well as cuestas, hogbacks, and several canyon and valley types (Hawley 1986).

The southern Colorado Plateau has both the highest and lowest elevations of the entire Colorado Plateau: the 3,851 m summit of Mt. Humphreys near Flagstaff, Arizona, and the 360 m low point where the Colorado River exits the Grand Canyon.

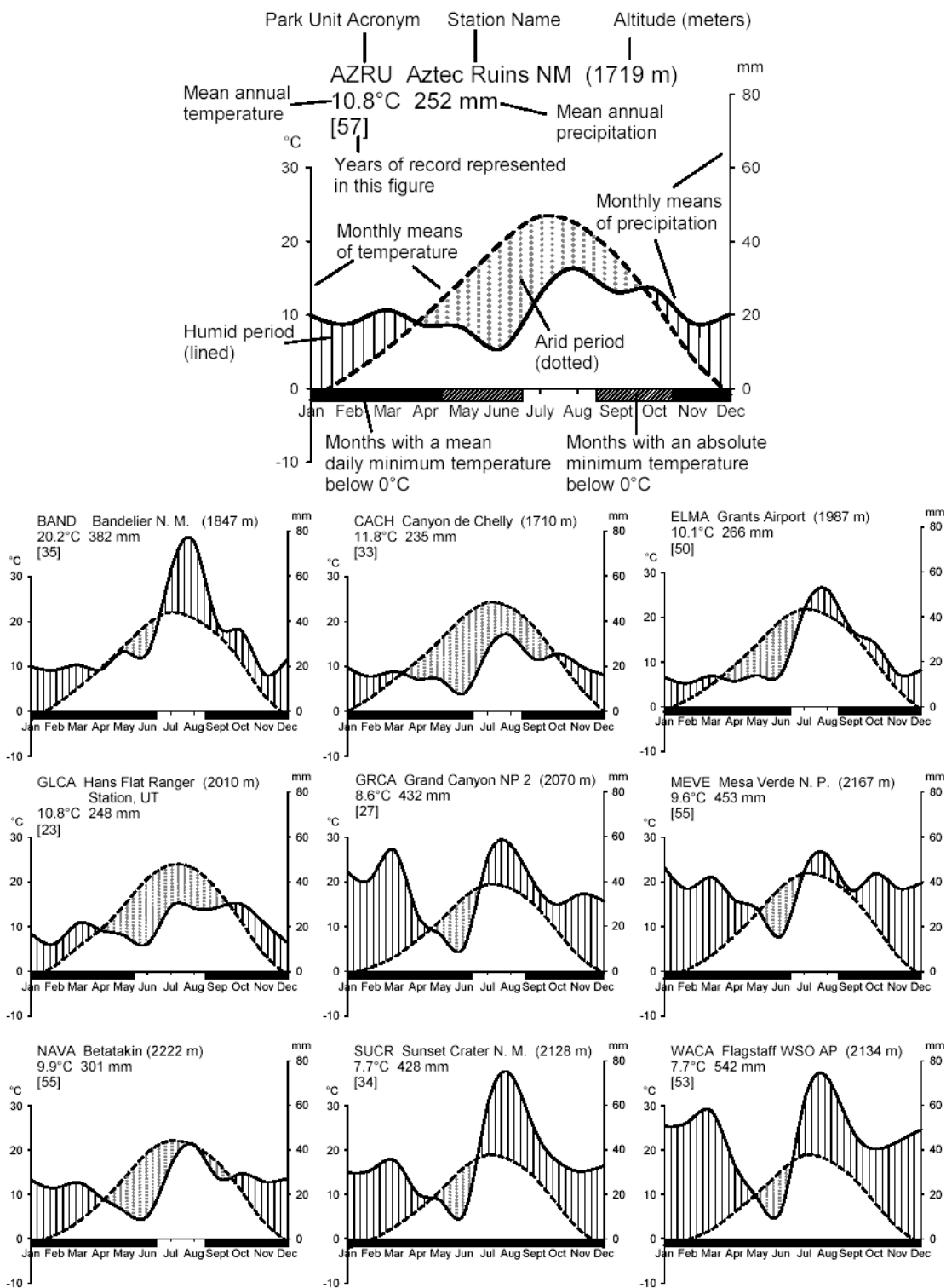
The higher elevations of this range, where montane and subalpine ecosystems occur, are uncommon in the southern Colorado Plateau. Even within SCPN, elevations over 1,750 m account for only 27% of the total area (unpublished SCPN data). Therefore, especially the subalpine ecosystems occur mostly as widely scattered areas, representing ecological islands in a sea of lower elevations.

Much of the montane and subalpine landscape has varied topography. Even an area such as the North Rim region of GRCA, which is considered relatively flat, has diverse topography. Topographic variations involving differences in elevation, slope aspect, slope inclination, and slope position are correlated with the distribution of ecosystems, their component species, and their disturbance regimes ([Figure 1](#); e.g., White and Vankat 1993).

Climate

Not only is the climate across the Colorado Plateau heterogeneous ([Figure 2](#); Richmond 1987, Mock 1996), but it is also difficult to characterize, except in broad terms, because there is a low density of climate stations and large elevational differences among them (Anderson et al. 2000). -

Figure 2. Climate diagrams (Walter 1963) for the nine units of SCPN with montane/subalpine ecosystems. Data are from National Weather Service Cooperative Network Stations (see <http://www.wrcc.dri.edu/climsum.html>)



In general, winters in the montane and subalpine ecosystems of the southern Colorado Plateau tend to be cold, summers warm to cool, and precipitation bimodal with peaks in winter and mid-summer. Winter precipitation falls as snow and a substantial snowpack develops, especially in the subalpine zone (Moir 1993). Precipitation decreases as temperatures warm in the spring, and early summer tends to be the driest time of the year. With the beginning of the monsoon season in early July, precipitation increases. After the monsoon season ends in late August or early September, precipitation decreases and temperatures cool.

The major trends within the southern Colorado Plateau are increases in precipitation and decreases in temperature from low to high elevations, as well as decreases in monsoonal precipitation from south to north (Higgins et al. 1997).

Winter weather is usually influenced by a high pressure system in the western United States, but this system is sometimes displaced over the Pacific Ocean, allowing low-pressure storms from the northeast Pacific Ocean to move southward before entering the continent along a southerly displaced jet stream and to pass over the Colorado Plateau (Betancourt and Biggar 1985, Petersen 1994, Weng and Jackson 1999). Typically, after this air-flow pattern is established, several successive winter storms pass over the southern Colorado Plateau (Petersen 1994). Winter storms typically are larger and last longer than summer storms.

In spring and early summer, the southern Colorado Plateau is influenced by a high pressure system, accounting for greatly reduced precipitation in June. However, warm moist air masses move into the southern Colorado Plateau from Mexico around July 1 and begin the monsoon season. Precipitation abruptly and dramatically increases, primarily from convection off heated surfaces but also from convergence and orographic lifting (Petersen 1994). Monsoonal storms typically show no frontal development but consist of small clusters of convective cells and therefore are scattered, often-brief precipitation events. Nevertheless, summer precipitation is less variable in timing and amount than winter precipitation. Monsoonal storms bring water vapor from the Gulf of Mexico and the Gulf of California (winter precipitation from the Pacific Ocean).

A critical component of the climate of the southern Colorado Plateau is the high frequency of lightning which poses an abundant source of forest fire ignitions. For example, an area of 7,756 km² in the Jemez Mountains of New Mexico (including BAND) annually received 1.2-3.0 cloud-to-ground lightning strikes/ha from 1985 to 1994 (Allen 2002). Lightning in that area peaked with the convective storms of the summer monsoon season, but was recorded every month of the year, and was especially impactful (in terms of fire ignitions) in the dry months of May and June.

Of course, weather patterns vary on annual and longer time scales. One important (especially in terms of fire frequency) longer time-scale variation is the development of weather conditions related to the El Niño-Southern Oscillation (ENSO) (Swetnam and Betancourt 1990, 1998). El Niño events occur on average once every 3-4 years and typically last 12-18 months. They bring cooler, wetter winters to the Southwest, including the southern Colorado Plateau (D'Arrigo and Jacoby 1991), while monsoonal rainfall tends to be normal or above normal (Hereford and Webb 1992). In contrast, La Niña events tend to bring drier winters. Such climatic variation has occurred in the Southwest for at least the last 2,000 years (Meko et al. 1995, Grissino-Mayer 1996, Grissino-Mayer et al. 1997). Century-scale climate changes have also been linked to changes in fire regimes, with drier centuries having more frequent, predominately mid summer fires and wetter centuries having less frequent, predominately late spring fires (Grissino-Mayer and Swetnam 2000).

Soil

The soils of the montane and subalpine ecosystems of the southern Colorado Plateau are as diverse as the topography and climate that produced them. Parent material tends to have less of an influence at these high elevations (Maker and Saugherty 1986) or, in comparison to studies of the effects of topography, climate, and disturbance, is understudied (Peet 2000). Betancourt (1990) considered elevational limits to be higher on limestone than on volcanic or metamorphic - parent materials and described elevational anomalies based on parent material for the La Sal Mountains just north of the

southern Colorado Plateau.

In general, montane and subalpine soils tend to be leached, acidic, and well developed (Maker and Saugherty 1986), as well as well-drained and ranging from shallow to deep and from fine to moderately coarse textured (Hendricks 1985). In addition, the soils have been formed in residuum (occasionally colluvium or alluvium) from volcanic materials or sandstone, limestone, or igneous rocks (Hendricks 1985).

In terms of classification, the soils fall into three orders (and one suborder of each): Alfisols (Boralfs), Mollisols (Borolls), and Entisols (Orthents) (Hendricks 1985, Maker and Saugherty 1986).

Alfisols tend have light-colored surface layers and clayey subsurface horizons. The Boralfs suborder develops in cool and cold mountain regions, often with Borolls (see below), but with less organic matter. Nutrient availability is at least moderate. Boralfs present include Typic Glossoboralfs, Mollic Eutroboralfs, and Typic Eutroboralfs.

Mollisols have deep, dark-colored surface horizons with high organic matter. The Borolls suborder develops in cool and cold mountain regions and has more organic matter than Boralfs (see above). Borolls present include Typic Argiborolls, Argic Cryoborolls, Argic Pachic Cryoborolls, and Lithic Cryoborolls.

Entisols have little or no evidence of horizon development, except for thin surface horizons with some organic matter. They are more likely to reflect the properties of the parent material than are Alfisols and Mollisols. In addition, Entisols tend to be high in nutrients. The Orthents suborder forms on moderate to steep slopes where the parent material is near the surface. Soil material is eroded faster than profile development on such sites, so these soils tend to be shallow (generally <50 cm). Orthents present include Typic Cryorthents and Typic Ustorthents.

In more detail, the montane and subalpine ecosystems of the southern Colorado Plateau in Arizona occur on frigid subhumid soils, divided into seven soil associations (Hendricks 1985). The equivalent portion of the southern Colorado Plateau in New Mexico has 20 associations (Maker et al. 1978).

Disturbance

Many attributes of the montane and subalpine ecosystems of the southern Colorado Plateau, including their structure, composition, and distribution, are dramatically affected by disturbance. In particular, most disturbances enhance the heterogeneous nature of montane and subalpine landscapes. Major agents of disturbance at the stand (patch) scale in these ecosystems are fire, wind, pests, and pathogens.

Fire

Given the relatively dry climate of much of the Southwest and the high frequency of lightning (Allen 2002), fire has had a major influence on montane and subalpine ecosystems of the southern Colorado Plateau. Moreover, fire appears to have been important, at least in the Jemez Mountains of northwestern New Mexico, for at least the last 8,000 years (Brunner Jass 1999). In recent times, the National Forests of Arizona and New Mexico have had the highest rate of lightning fire ignitions in the United States (Barrows 1978 in Allen 2002). However, the role of fire has differed among ecosystems, with elevation and its associated gradients in precipitation, evapotranspiration, fuel moisture levels, etc. being major determinates of the fire regimes of individual ecosystems.

The fire regime of an ecosystem or a geographic location refers to factors such as the frequency, intensity, timing, and distribution of fires. Basic descriptors of fire regimes include quantitative measures such as mean fire return interval (mean time between fires in the study area) and fire turnover or rotation (time to burn an area equivalent in size to the study area). Fire regimes are also characterized qualitatively with such terms as surface, crown, and mixed severity fire regimes.

Surface fires are high-frequency, low-intensity fires, which, in the Southwest prior to fire exclusion, typically had a mean fire interval of a few decades or less. Given their low severity, surface fires

generally did not initiate succession at patch and landscape scales, but of course affected plant population dynamics.

Crown fires are low-frequency, high-intensity fires, which typically had a mean fire interval of at least a century. Their high severity removed the forest canopy, thereby initiating succession at patch and landscape scales. Indeed, such fires are often referred to as stand-replacement or stand-initiating fires.

Mixed severity fires burn as low-intensity surface fires in some areas within a landscape and become high-intensity crown fires in other areas of the landscape. Such fires initiated succession only at the patch scale and only in areas of crowning.

Prior to Euro-American influence on southwestern forest ecosystems, periodic surface fires characterized the montane elevational zone from the Ponderosa Pine Forest into the Mixed Conifer Forest. Augmented by the dry conditions of these lower elevations, surface fires burned through the fine fuels of herbaceous plants and relatively loose flammable ponderosa pine needle litter. After burning, the fire-adapted herbaceous plants and needle litter regenerated in only a few years, providing fuel for another surface fire (Allen 2002).

In higher-elevation Mixed Conifer and Spruce-Fir Forests, fires were less frequent as a result of moister conditions, sparser herbaceous layer, and more compacted, less flammable leaf litter. Consequently, fuels increased between fires such that, when fires did burn, they tended to be crown fires. Stands of Montane Shrubland (at lower elevations) also were characterized by crown fires (see *Montane Shrubland Ecosystem*).

The history of fires in montane ecosystems is known for the past several centuries for several areas. Most investigators examined fire scars left in the wood of old trees (cf. Swetnam and Baisan 1996), but this approach likely overestimates the frequency of fires (Baker and Ehle 2001). Also, this method is less useful in forests where crown-fires have occurred, such as subalpine ecosystems, because remnant, scarred trees are uncommon or absent. The history of crown fires in Montane Shrublands has been studied by determining the age of cohorts of stems originating as sprouts after fire (cf. Floyd et al. 2000).

Wind

Less research has examined the effects of wind on montane and subalpine ecosystems of the southern Colorado Plateau. Nevertheless, wind events at scales from microbursts involving small-scale, severe downdrafts to large storms occasionally result in tree blowdowns in forested areas. Blowdowns over large areas have been most thoroughly described for subalpine forests (see *Spruce-Fir Forest Ecosystem*), but Allen (1989) reported a major blowdown in Ponderosa Pine Forest in and near BAND.

In general, the disturbance regime of strong winds can be considered to be low-frequency, high-intensity, and such winds can initiate succession at stand or smaller scales and at least impact plant population dynamics. Winds are likely to have greatest impact in winter when winds tend to be stronger (at least in the alpine zone; Glidden 1981, 1982 in Veblen et al. 1991a) and tree branches are snow-covered.

The history of wind damage in montane and subalpine ecosystems is largely limited to slightly more than the last century -- the period of exploration and photography.

Pests and Pathogens

The major pests and pathogens impacting montane and subalpine ecosystems of the southern Colorado Plateau are native species long present in the region. Therefore, presumably these species co-evolved with the biota. The key insect pests are bark beetles and defoliating insects. The most important pathogens are root decay fungi.

Bark beetles and defoliating insects are continuously present in montane and subalpine forest ecosystems, but their populations are usually small. Only occasionally do they rapidly increase to where their effects are obvious to casual observers. Root decay fungi also are continuously present, but their population dynamics are not so pronounced or so rapidly changing as to be obvious.

Bark beetles include several species, most of which are restricted to specific species of trees. According to Dahms and Geils (1997), the host trees and their most common bark beetle species in the Southwest are

ponderosa pine: roundheaded pine beetle (*Dendroctonus adjunctus*), western pine beetle (*D. brevicornis*), mountain pine beetle (*D. ponderosae*), pine engraver (*Ips pini*), and the Arizona fivespined ips (*I. lecontei*)
Douglas fir: Douglas fir beetle (*Dendroctonus pseudotsugae*)
white fir: fir engraver (*Scolytus ventralis*)
Engelmann spruce: spruce beetle (*Dendroctonus rufipennis*)
subalpine fir: western balsam bark beetle (*Dryocoetes confusus*)

These beetles are usually present in low numbers, persisting in less productive living trees and in fresh windthrows, occasionally resulting in tree death. However, outbreaks occur periodically and, especially in stressed stands, can result in high mortality of trees, especially larger, older trees.

Defoliating insects include fewer species, and the primary one, western spruce budworm (*Choristoneura occidentalis*), is not specific in its hosts. Although it attacks many species in western North America, it impacts primarily white fir and Douglas fir in the Southwest (Dahms and Geils 1997). When outbreaks last several years, complete defoliation can occur and, if sustained, results in reduced vigor and tree death. In contrast to mortality from bark beetles, mortality tends to be greater in smaller trees of the understory.

The other major defoliating insect in the Southwest is the western tent caterpillar (*Malacosoma californicum*). Annual and biannual defoliation of quaking aspen for several consecutive years has been reported to minimize tree growth and result in some mortality (Allen 1989).

Root decay fungi are common in the Southwest (Dahms and Geils 1997). The host trees and their most common root decay fungi in the Southwest are

ponderosa pine: *Heterobasidion annosum*
Douglas fir: *Phaeolus schweinitzii*
white fir: *Heterobasidion annosum*
Engelmann spruce: *Inonotus tomentosus*

In addition, *Armillaria* spp. affect nearly all tree species. Root disease weakens trees, increasing the likelihood of bark beetle infestation and windthrow. Large canopy trees are more likely to be impacted, especially on mesic sites

Vegetation Dynamics

Vegetation dynamics refer to the response of vegetation to disturbance and include everything from small shifts in the size and structure of populations to landscape scale succession. Given the ubiquity of disturbance in montane and subalpine ecosystems in the southern Colorado Plateau, vegetation dynamics are also ubiquitous.

Vegetation dynamics are especially obvious when they involve succession, i.e., the sequential replacement of species over time in response to disturbance. Succession occurs at various scales, but only the stand and landscape scales are discussed here (for a discussion of succession on the individual-tree scale, see *Ponderosa Pine Forest Ecosystem*).

Succession at the stand scale was formerly thought to involve highly predictable, progressive change to an equilibrium condition called the climax stage of succession. More contemporary views consider succession to be a stochastic process, i.e., one based on probabilities and therefore not entirely predictable because chance plays an important role. Consequently, succession currently is viewed as less than completely predictable and progressive and leading to a late-successional, non-equilibrium

stage subject to variation resulting from numerous factors including the disturbance regime.

Succession at the landscape scale also was formerly viewed as resulting in equilibrium conditions either across the entire landscape or in the proportions of different successional ages of stands making up the landscape mosaic. More contemporary views recognize that disturbance is pervasive at varying scales, intensities, frequencies and environmental conditions are always shifting. Therefore, landscapes currently are viewed as ever-changing, i.e., in non-equilibrium.

The descriptions of succession in the sections on individual ecosystems, especially in the conceptual models, treat succession as occurring in stages. However, just as ecosystems vary continuously along spatial and environmental gradients, ecosystems also vary continuously along temporal (successional) gradients.

Paleoecology

The paleoecology of the Southwest is as well, if not more thoroughly, studied than any region on earth (Betancourt et al. 1990, Swetnam et al. 1999, Allen 2002). Therefore, there is a substantial literature on paleoecology, and an understanding of montane and subalpine ecosystems of the southern Colorado Plateau is becoming increasingly clear as additional sites of pollen deposition and pack rat middens are investigated and as paleoclimate research reveals the driving forces behind long-term ecosystem change. The GRCA area of Arizona and the Jemez Mountain region around BAND have been studied especially intensively (Cole 1982, 1985, 1990, Weng and Jackson 1999, Allen 2002).

The major taxa that characterize today's biotic communities of the Southwest have been in place since the end of the Tertiary, about 2 million years (Lowe and Brown 1994). However, the distribution of these taxa has changed many times in both elevation and latitude in response to climate. During these shifts in distribution, the Colorado Plateau played a key role in the biogeography of the Southwest, as the Colorado Plateau provided a connection between the Rocky Mountains and regions to the west and south (Anderson et al. 2000). Moreover, it appears that the species of the Southwest responded quickly compared to gradual responses of forest taxa in central and eastern North America, because mountains provided refugia and sources of species during climatic fluctuations (Van Devender and Spaulding 1979). An important aspect of the shifts in distribution is that species migrated individually rather than as species assemblages or communities (Van Devender and Spaulding 1979, Cole 1985). Another important aspect of the shifts is their influence on local extinctions and colonizations of species (Betancourt 1990).

Full-Glacial (ca. 21,000-13,000 yr BP)

As with all ecosystems in temperate and boreal North America, montane and subalpine ecosystems of the southern Colorado Plateau were dramatically affected by Pleistocene glaciation. While of course details are sketchy for the whole southern Colorado Plateau (and details differ among sites), in general full-glacial (mid-Wisconsin) winters had more precipitation and full-glacial summers had lower temperatures and less monsoon precipitation than today (Betancourt 1990, Petersen 1994, Anderson et al. 2000). Temperature gradients were steeper both latitudinally and elevationally in western North America (Petersen 1994).

Computer simulations suggest that much of difference with today's climate was related to a southerly displacement of the jet stream (Van Devender and Spaulding 1979, Thompson et al. 1993, Petersen 1994, Barlein et al. 1998). For example, the jet stream in January was likely positioned over northern Mexico (instead of its present position in southern Canada). This brought Pacific air masses across the Colorado Plateau more frequently, which accounted for increased precipitation, greater cloud cover, and generally cooler temperatures (Petersen 1994). The southerly position of the jet stream also likely inhibited development of a monsoon season, but other contributing factors were heavier snowpacks on the Colorado Plateau and southern Rocky Mountains, lower sea levels, and colder oceanic conditions in tropical areas (Anderson et al. 2000).

During the full-glacial period of cooler temperatures and greater winter precipitation, the species of

today's montane and subalpine forest ecosystems generally occurred at lower elevations than today, or, in the case of ponderosa pine, may have been absent. For example, species from today's Spruce-Fir and Mixed Conifer Forests occupied mid-elevations that now have Ponderosa Pine Forest (Anderson et al. 2000). Also, montane forests of Douglas fir, southwestern white pine (*Pinus strobiformis*), and white fir covered most of New Mexico (Dick-Peddie 1993).

More specifically, a mixed forest of Engelmann spruce, white fir, and Douglas fir with an understory of sagebrush (*Artemisia*), grasses (Poaceae), and composites (Asteraceae) was present during the full-glacial near the Mogollon Rim in the southern Colorado Plateau of Arizona (Anderson 1993). Later, Engelmann spruce dominated as white fir and Douglas fir decreased. Today, this area has extensive Ponderosa Pine Forest.

Further north in the GRCA area, the climate was colder throughout the year, was less temperate, and had more winter precipitation (although the mean annual precipitation was similar to today) (Cole 1985). Most plants occurred 600-1,000 m below their current positions (Cole 1985, 1990), as did arthropods (Elias et al. 1992). Forests occupied elevations over approximately 1,450 m (alpine tundra was present on the highest elevations of the Kaibab Plateau; Weng and Jackson 1999). Low and mid elevation forests were dominated by limber pine, white fir, and Douglas fir, and ponderosa pine was absent. High elevation forests above about 2,000 m were dominated by spruce. The absence of ponderosa pine is often interpreted as suggesting a paucity of summer precipitation (Betancourt 1990, Cole 1990).

At a high elevation (2,778 m) site on the Kaibab Plateau north of the GRCA boundary, alpine tundra was present before about 12,900 yr BP (before present), with treeline only slightly lower (Weng and Jackson 1999). A somewhat lower site (2,518 m) had a spruce woodland that probably was dominated by Engelmann spruce.

In the area of CACH, blue spruce, limber pine, Douglas fir, common juniper, and Rocky Mountain juniper (*Juniperus scopulorum*) occurred at least as low as 1,770 m (Betancourt and Davis 1984), and, as elsewhere on the southern Colorado Plateau, ponderosa pine was lacking.

Late Glacial and Early Holocene (ca. 13,000-8,500 yr BP)

Computer simulations indicate that the shrinking of continental ice masses led to a northward migration of the jet stream (Van Devender 1977, Thompson et al. 1993, Petersen 1994). This more northerly storm track resulted in increased temperatures in the Southwest and led to the development of a summer monsoon season, shifting the precipitation regime from winter-dominated to summer-dominated (Betancourt and Biggar 1985, Weng and Jackson 1999). High summer insolation augmented subtropical highs, producing significant summer precipitation in the early Holocene, making it cooler and wetter than today (Weng and Jackson 1999).

With the changing climate, there were rapid changes in species and communities as species began migrating toward the higher elevations of modern conditions. In general, above 2,200 m on the Colorado Plateau, fir forest replaced spruce forest, and at 1,900-2,100 m, ponderosa pine, Douglas fir, and Utah juniper replaced mixed coniferous forest (Anderson et al. 2000). Ponderosa pine spread rapidly across the mid elevations of the southern Colorado Plateau (Anderson 1989), but it is unclear whether it migrated from the south or expanded from isolated small populations (Betancourt and Davis 1984). The spread of ponderosa pine may have been related to increased summer, monsoonal precipitation (Anderson 1989, 1993, Betancourt 1990, Cole 1990), although a change in the fire regime with more lightning ignitions in the summer may have been the critical factor (Betancourt 1990).

Near the southern edge of the Colorado Plateau in Arizona (the Mogollon Rim), the Engelmann spruce-dominated forest was replaced by a forest of ponderosa pine similar to that currently present (Anderson 1993).

In GRCA, Douglas fir and white fir increased in elevation (but were still at least 350 m below current ranges) and ponderosa pine was present (Cole 1982). The lower limit of forested elevations rose from about 1,450 to 1,750 m (Cole 1985). It has been argued that such elevational shifts should be viewed in

a broader perspective, as associated with latitudinal shifts (Cole 1990). North of GRCA on the Kaibab Plateau, tundra was replaced at the highest elevations by Engelmann spruce and subalpine fir, and in turn these were replaced by blue spruce and later mixed forests of blue spruce, subalpine fir, ponderosa pine, and, later, Douglas fir (Weng and Jackson 1999). Aspen was likely present too. At a somewhat lower elevation study site, the full-glacial spruce woodland was replaced by a denser forest dominated by blue spruce, but this soon was rapidly replaced by ponderosa pine (aspen was also relatively abundant). Fire frequency greatly increased at the time of establishment of ponderosa pine.

Middle and Late Holocene (8,500 BP to present)

The middle Holocene experienced on-going increases in temperature and decreases in effective precipitation, before a period of climatic variability. For example, the middle Holocene was dry and warm, but wet and cool conditions returned in the late Holocene (Dick-Peddie 1993, Hasbargen 1994, Weng and Jackson 1999).

The vegetation continued to change toward modern conditions, with fluctuations that matched variations in the climate. Various estimates for the establishment of modern vegetation exist. Expressed in years BP, they include: 11,000 (Van Devender and Spaulding 1979), 10,400 (Anderson 1993), 9,500 (Anderson et al. 2000), 6,000 (Cole 1985, Thompson et al. 1993, Hasbargen 1994), 5,000 (Murdock 1994), and 4,000 (Weng and Jackson 1999). These various dates may represent differences in authors' definitions of similarity to modern conditions, as well as site-specific differences.

Land-Use History

The land-use history of any geographic region is one of the formative factors in the present-day structure, composition, and function of the region's ecosystems. This appears especially true for most, but not all, of the montane and subalpine ecosystems of the southern Colorado Plateau. Human land uses in these ecosystems have ranged from subsistence hunting and gathering to resource exploitation, resource protection, and ecologically based resource management.

The thousands of years of human land use in the southern Colorado Plateau can be divided into two major times. The first is when Native Americans dominated land use. It is much the longer of the two, but it is also much less well known. The second is when Euro-Americans dominated land use, and it covers only about the last one and one-half centuries.

Native American Dominance of Land Use

Compared to other regions of the world, human history of the Southwest is relatively brief. Although Native Americans are commonly thought to have had little impact on their environment, except for land management by fire, evidence suggests this is a myth (Dahms and Geils 1997). Perhaps the following statement accurately describes the impact of Native Americans across landscapes (Vale 1998):

The pre-European landscape of North America was both pristine and humanized, varying through space and time and degree of conformity to the extreme conditions represented by purely naturalistic and purely anthropogenic.

History

Humans first entered the Southwest at least 11,000 yr BP. Archeologists refer to these first inhabitants as Paleo Indians. Little is known about these hunting-gathering people; however, they likely occupied primarily high plains (Lister and Lister 1994), had low population densities, and moved frequently to follow game, especially large mammals. Therefore, except for a possible role in the extinction of the Pleistocene megafauna (Martin and Klein 1984), it is likely that they had little lasting impact on ecosystems of the region (Allen 2002), especially on montane and subalpine ecosystems.

Between 8,000 and 10,000 yr BP., the megafauna hunted by the Paleo Indians became extinct and drier conditions led to the movement of remaining animals eastward into the Great Plains. Many of the Paleo Indians followed this movement.

The Paleo Indians of the Southwest were gradually replaced by the Desert Archaic peoples who immigrated from less hospitable environments. These peoples were also hunter-gatherers, but utilized plants more than the Paleo Indians. The Desert Archaic peoples were seasonally migratory, entering high elevation regions in the summer to hunt deer and elk and to gather wild foods. Because climate and vegetation had become more similar to present day conditions (see *Paleoecology*), the Desert Archaic peoples appear to have been the first Native Americans with the potential to have impacted the direct predecessors of today's montane and subalpine ecosystems of the southern Colorado Plateau. However, their impacts are presumed to have been localized and temporary, as these migratory people would have moved whenever resources became scarce (Allen 2002). Although it has been speculated that they used fire as an ecological management tool (Fish 1996), this has been questioned because of the lack of direct supporting evidence (Allen 2002).

By about 4,000 yr BP, corn was brought into the Southwest from Mexico, and later was followed by squash and beans. The Mogollon highlands of the southern Colorado Plateau may have been important in the transition of corn from Mexico because its environment was similar to that of the highlands of central Mexico where corn had evolved (Lister and Lister 1994). Despite the beginnings of agriculture, the Archaic peoples continued primarily as hunter-gatherers with a seasonal pattern of migration.

Only gradually did agriculture play an increasingly important role for Native American peoples of the southern Colorado Plateau. As peoples became more committed to agriculture, relatively permanent hamlets and villages became common. With settlements, the potential for humans to alter landscapes increased. However, villages tended to be in areas of the Pinyon-Juniper Woodland (Allen 2002), which is at mid to lower elevations where longer growing seasons facilitated agriculture (Bremer 1989). Therefore, sedentism would seem to have had little effect on montane and subalpine ecosystems and may have resulted in decreased use of these high elevation ecosystems.

About 1,000 yr BP, nomadic peoples from western and northern areas moved into the southern Colorado Plateau. For example, Southern Paiutes began occupying portions of the GRCA area, mostly north of the Colorado River, by about 600-700 yr BP (Madsen 1975). They were hunter gatherers with a seasonal migration pattern, who also planted fields in drainage bottoms. The Southern Paiute hunted deer, elk, antelope, and bighorn sheep on the Kaibab Plateau, as well as small game including rabbit, chipmunk, deer mouse, muskrat, rat, beaver, and porcupine (Stoffle and Evans, 1976). Further west in the GRCA region, ancestors of the Havasupai and Hualapai appeared about 700 yr BP. The Pai groups also were hunter-gatherers who hunted on the region's forested plateaus.

The area of BAND was heavily utilized by Native Americans from about 1150 to 1550 A.D., with 1,000-3,500 people in an area of about 100 km² (Orcutt 1999 in Allen 2002), with archeological sites concentrated in the Pinyon-Juniper Woodland and lower-elevation sites of Ponderosa Pine Forest. The local impact of this population was substantial, but it is unclear if they affected higher elevations (Allen 2002).

The first Europeans thought to have entered the Colorado Plateau comprised an exploring party headed by a Franciscan, Fray Marcos de Niza. In 1539, they reached what is believed to have been a Zuni village in New Mexico. His party was followed by a Spanish exploring party led by Francisco Vazquez de Coronado in 1540. Accompanying Coronado were large flocks of cattle and sheep, the first entry of livestock into the United States (Haskett 1935, 1936).

The first European settlements on the Colorado Plateau were established by Spaniards. Although these settlements did not endure, the introduction of livestock by Spaniards left a large and lasting impact on the land. Some Native American peoples adopted sheepherding into their cultures as early as the 17th century, and by 1757 New Mexico had 112,000 sheep and goats (excluding those owned by Navajos), over half of which were owned by Native Americans (Bailey 1980, Baxter 1987).

Euro-American fur trappers and traders began to enter the Colorado Plateau by perhaps the 1820s (Brown et al. 1994), and were the only Euro-American explorers in much of the first half of the 19th century.

In the mid 19th century, various United States military surveying expeditions visited the Colorado Plateau to consider possible routes across the Southwest (Wurtz 1991). These were followed by other governmental surveys designed to evaluate the natural resources of the region.

The first lasting Euro-American settlements on the Colorado Plateau were established by Mormons (Wurtz 1991). Initially, they settled areas just off the Colorado Plateau, including towns such as Cedar City and Saint George in southwestern Utah. These towns became bases for settlements on the Plateau itself (Greer 1981), the first permanent settlements of which were in the Arizona Strip north of the Grand Canyon in the 1860s (Wurtz 1991).

Permanent Euro-American settlements marked the impending end of Native American dominance of land use in much of the southern Colorado Plateau. Although Native American land use continues to dominate large portions of the region today, it does not directly affect montane and subalpine ecosystem within SCPN units. Past and contemporary land use patterns differ among regions of the southern Colorado Plateau, depending on which cultural group inhabited which area (Parker 1991). Indigenous cultures of the western portion of this region are the Hualpai, Havasupai, and Southern Paiute cultures. In the central portion are the Hopi and Navajo cultures. In the east are the Ute and Jicarilla Apache cultures.

Impacts on the Landscape

Burning - Native American peoples set fires for hunting, improving yields from wild food crops, and other reasons for thousands of years in many North American landscapes (Pyne 1997). Their fires are thought to have altered the structure and composition of some forests and other ecosystems. The question of whether Native Americans used fire as a landscape-scale tool in the Southwest has been controversial. However, a recent review concluded that direct evidence of Native American use of fire as a landscape tool in the Southwest is lacking (Allen 2002). More specifically, detailed review of ethnographic literature pertinent to BAND revealed no information on broad-scale use of fire by Native Americans (Levine and Merlan 1997 in Allen 2002). The lack of hard evidence and the concentration of Native American populations at lower elevations make it especially unlikely that landscape-scale fires were set by Native Americans in the montane and subalpine ecosystems of the southern Colorado Plateau.

In some areas, the lack of clear evidence of Native American burning may reflect the lack of a need to burn, given the high frequency of lightning fires in many forests of the region. For example, areas in GRCA such as the Powell and Walhalla Plateaus were densely occupied by Native Americans, but are also areas of frequent lightning ignitions. It is possible that the open forests of such areas were an attraction for Native Americans (for better hunting, gathering, and agriculture) rather than a product of Native American land use (Leatherbury 2003).

In consort with the lack of evidence of Native American burning, research has indicated that the high incidence of lightning in the Southwest is sufficient to account for the fire regime prior to Euro-American influence (Swetnam and Baisan 1996). In a recent review, Allen (2002) concluded that Native Americans increased fire frequencies or otherwise altered fire regimes for limited time periods in some small areas (cf. Kaye and Swetnam 1999); however,

...the available [archaeological, ethnographic, and fire-scar chronology] evidence indicates that Indians likely had minimal effects on the fire regimes of most upland ecosystems in the Southwest prior to European contact.

Other - Although it appears that Native Americans did not burn the montane and subalpine ecosystems of the southern Colorado Plateau at the landscape scale, Native Americans had other, smaller-scale impacts.

For example, trees were cut for fuel, shelter, and clearing for agriculture. Needs for fuel and small shelters often likely were met by cutting pinyon pines and junipers, which were abundant in the mid-elevations of many settlements. However, larger structures required logs from ponderosa pine and other

species. Some structures were supported by thousands of logs hauled great distances (Betancourt et al. 1986). The impact of tree cutting must have been substantial in some areas.

In addition, areas were cleared for agriculture (but usually at lower elevations) and inner bark exposed by stripping the outer bark from ponderosa pines was used as a food source (Swetnam 1984, Kaye and Swetnam 1999). Hunting also likely affected montane and subalpine ecosystems. Populations of elk in particular may have been reduced by early Native American hunters (Allen 1996). The impact of livestock grazing by Native Americans is covered in the next section.

Euro-American Dominance of Land Use

The Southwest has one of the longest records of presence of Europeans and Euro-Americans of any region of North America. Early Europeans and Euro-Americans had few impacts, consequently the transition from Native American to Euro-American dominance of land use took over three centuries (cf. Wurtz 1991).

History

The emergence of Euro-American dominance of land use on the southern Colorado Plateau was aided primarily by the development of transportation routes (Wurtz 1991). For example, in 1854 Jacob Hamblin developed a road from St. George in southern Utah across the Arizona Strip. This aided in the settlement of areas such as Pipe Springs, Arizona, near the Kaibab Plateau. Further south, U.S. Army Lieutenant Edward Beale completed a road in 1859 that crossed the southern Colorado Plateau along the 35th parallel.

Construction of the Beale Wagon Road had a major impact on Euro-American settlement and land use on the southern Colorado Plateau because it provided a route for Euro-Americans to drive livestock (Haskett 1936). This greatly increased the rate of conversion from Native American to Euro-American dominance of land use on the southern Colorado Plateau.

Extending the impact of the wagon road was construction of a railroad across the southern Colorado Plateau. The first tracks were laid on the Colorado Plateau in 1881 by the Atchison Topeka and Santa Fe Railroad (Wurtz 1991). Construction of the railroad led to the first widespread logging on the southern Colorado Plateau, as railroad ties were needed to lay track.

Completion of the railroad in 1883 brought an influx of ranchers and homesteaders into the area (Cline 1976). The railroad also opened new markets for livestock. Although estimates of historical livestock numbers are unlikely to be accurate (different sources provided vastly different numbers), sheep in Arizona reportedly increased from about 77,000 head in 1880 to nearly 700,000 head in 1890, not including sheep grazed by Native Americans (Haskett 1936). During the same time, cattle increased in Arizona from 36,000 to 263,000, although other records indicate over 600,000 head were grazing in 1890 (Haskett 1935). By 1894, over 200,000 sheep were being grazed on just the Coconino County portion of the southern Colorado Plateau (Haskett 1936). Dramatic increases in livestock in New Mexico also first occurred in the 1880s (Denevan 1967), with over 5 million reported in 1890 (Wootton 1908 in Allen 2002).

Concern over increasing intensive, destructive, and widespread land uses led to establishment of Forest Reserves (precursor of today's National Forests), Game Preserves, and units of the National Park System on the southern Colorado Plateau beginning in the 1890s. Land use in areas eventually managed by the National Park Service shifted from resource exploitation to a focus on resource protection, in which land management practices such as fire exclusion and predator control dominated. With the establishment of units of SCPN, tourism dramatically increased. Beginning in the 1960s, NPS management became more ecologically oriented and included such practices as reintroducing fire into landscapes long kept free of fire.

Impacts on the Landscape

The major effect of Euro-American land use on the montane and subalpine ecosystems within SCPN was an abrupt and dramatic alteration of fire regimes. Several factors brought about the change. Euro-Americans may have provided an additional source of ignitions, but livestock grazing and fire exclusion

had greater impacts.

Source of Ignitions - Evidence of increased ignitions by Euro-Americans includes a first person description by John Wesley Powell in which he described having his campfire inadvertently start a crown fire (Powell 1890). While it is difficult to assess the frequency of such events, Euro-American exploration and settlement in the Southwest during the last half of the 19th century may have increased fire ignitions in Spruce-Fir and possibly Mixed Conifer Forests, where fire frequencies otherwise may have been limited by chance occurrence of lighting during brief dry periods; however, fire history studies do not indicate an abnormally high frequency of fires during this period (Allen 2002).

Livestock herders also have been said to have increased fire frequencies in montane and subalpine ecosystems of the southern Colorado Plateau (e.g., Allen 2002). However, evidence of increased burning hasn't been found in fire history studies, even for locations specifically described as having been burned by herders (Allen 2002). Therefore, it appears that herders were not unusually important sources of ignitions. In fact, fire-history studies typically show, not an increase in fire frequency with grazing, but rather an abrupt decline.

Livestock Grazing - As large herds of livestock were taken into montane and subalpine ecosystems of the southern Colorado Plateau in the mid-19th century, they greatly reduced formerly dense herbaceous layers of open forests and meadows (e.g., Dahms and Geils 1997). This decline of the herbaceous layer meant a loss of fine fuels that had carried surface fires through the forests. As a result, the frequency of fires abruptly and dramatically decreased (Swetnam et al. 1999). Several lines of evidence connect grazing with the change in fire regimes (Allen 2002). For example, substantial change in fire frequencies has not been found in isolated areas likely free of grazing, such as forested islands surrounded by lava flows in ELMA (Grissino-Mayer and Swetnam 1995, Touchan et al. 1995) and isolated plateaus in GRCA (Fulé et al. 2000). In addition, areas used by Native Americans for livestock grazing had early declines in fire frequencies (Savage and Swetnam 1990, Touchan et al. 1995).

Grazing also may have enhanced tree recruitment via reducing competition from the herbaceous understory (Belsky and Blumenthal 1997). Furthermore, trampling from grazing is thought to have dramatically affected soil properties by increasing compaction, reducing water infiltration rates, and increasing erosion (deBuys 1985, Belsky and Blumenthal 1997).

Fire Exclusion - As federal governmental agencies began managing land in the southern Colorado Plateau in the late 19th and early 20th centuries, land management practices focused on protection of resources.

At the time, it was generally accepted that fires were caused primarily by humans (Allen 2002). Fires were therefore viewed as unnatural events from which forests should be protected. Initial attempts at fire exclusion became widespread across the Southwest early in the 20th century (Pyne 1997). For example, Coconino National Forest cut fuel breaks up to 30 m wide as early as 1907-1908 and initiated fire lookouts as early as 1911 (Sawyer 1976). Fire exclusion on the North Rim of GRCA was evident by about 1920 (Wolf and Mast 1998). With technological advances, particularly with regard to the use of aircraft, fires were effectively excluded by the middle of the 20th century (Sawyer 1976, Swetnam 1990).

The reduction of fire frequencies in forests where fire had maintained generally open stand structure -- first inadvertently by livestock grazing and later by active fire exclusion -- caused the now well known dramatic changes in forest structures, fuels, and species compositions (see descriptions of the individual forest ecosystems). However, reduced fire frequencies may have had an even broader impact. For example, the change in the fire regime (followed by increasing tree densities and decreasing herb and shrub cover) is considered a factor in the precipitous decline of the deer population in and near the North Rim of GRCA in the 1920s (Mitchell and Freeman 1993).

Other - Although the over-riding impact of Euro-Americans on montane ecosystems of SCPN has been the reduction of fire frequencies, other historical land uses or land management practices also altered ecosystems.

Among these is predator control. Euro-American settlers and government land managers sought to kill predators to protect livestock and native ungulates. Units of SCPN had aggressive predator control programs, which included hiring government hunters. From 1906 to 1939 on the Kaibab Plateau in and near GRCA, predator control efforts resulted in the death of 7388 coyotes, 863 bobcats, 816 mountain lions, and 30 wolves (Rasmussen 1941). By 1930, wolves were extinct on the Kaibab Plateau (Mann and Locke 1931). The ecological impacts of predator control programs are not fully understood; however, predator control is thought to have been a factor in the population explosion of the deer herd in and near the North Rim of GRCA in the 1910s-1920s (Mitchell and Freeman 1993).

Tree cutting has also impacted montane forest ecosystems in SCPN units, albeit on a much more local scale than livestock grazing, fire exclusion, and predator control. In addition to tree cutting by Native Americans, early Euro-American settlers cut trees for shelter, corrals, and fuel. Tree cutting continued under NPS management, primarily for tourism infrastructure (lodging, roads, etc.) and for insect control.

Current Anthropogenic Stressors

Fire Exclusion

The historical aspects of fire exclusion are covered in *Land Use History*. The impacts of fire exclusion differed among ecosystems (see *Individual Ecosystems*).

Exotic Species

The presence of exotic species is closely linked to land use because the invasion of exotics is favored by disturbance (Elton 1958, Rejmánek 1989, Vitousek et al. 1996). Not all exotic species pose a threat (Williamson 1996), but some can interfere with ecosystems by altering species composition, structure, and function (Cronk and Fuller 1995, Vitousek et al. 1996). Worldwide, exotic species are considered a major threat to biodiversity, second only to habitat destruction (Randall 1996, Chornesky and Randall 2003).

Invasion of exotic species into a landscape involves four stages: introduction, dispersal, colonization, and establishment (Vankat and Roy 2002). Relative to a unit of SCPN, *introduction* refers to the appearance of the species in the region surrounding the unit, where it then has the potential to disperse directly into the unit. Much of the southern Colorado Plateau has been and continues to be subject to extensive human land uses that favor populations of exotic species.

Dispersal is the movement of the species into the SCPN unit itself. Visitors to each unit pass through the surrounding landscape and thus are potential vectors of dispersal as they inadvertently carry seeds or other units of dispersal attached to vehicles, clothing, camping equipment, etc. Therefore, dispersal generally occurs via road and river corridors.

Colonization is the growth and reproduction of the individuals dispersed into the SCPN unit. Colonizing populations are often small in size and extent, as well as restricted to a specific habitat. Colonization often occurs in areas of disturbance such as developed areas, roadsides, back country campsites, and burned areas.

Establishment is the spread of the species outside its area of colonization, often into other habitats of the SCPN unit. Establishment may be slow in areas that are in a natural or semi-natural state, but land use practices such as thinning and burning can promote establishment. Areas burned by wildfires are especially likely to be sites of establishment of exotic species (Crawford et al. 2001). Carefully designed monitoring and management practices can reduce if not prevent establishment, especially if they are designed to address all four stages of invasion, not just the establishment stage (Vankat and Roy 2002). For example, early detection and management of colonizing populations can be especially effective in preventing invasions.

Worldwide, the number of exotic species and their abundance have increased dramatically over the last century as human disturbance has become more widespread. In the United States, there are at least

50,000 introduced plant and animal species (Pimentel et al. 2000). Invasive plants infest >400,000 km² in the United States and increase by 8-20% annually (FICMNEW 1998). The Southwest does not have as many exotic species as other regions of the United States, primarily because extensive and intensive Euro-American land use began later in this region (Rejmánek and Randall, 1994). Nevertheless, the number of exotics in the Southwest has increased over the past several decades. For example, 190 exotic plant species were reported in Arizona in 1942 and 330 in 1991 (Bahre 1991).

Exotic species pose serious threats to the National Park System (Bratton 1982, Randall 1996), comprising up to 25% of the flora of some areas (Vitousek et al. 1996). In GRCA, for example, there are 169 known exotic plant species, comprising about 10% of the flora, compared to only 9 recorded in the earliest GRCA flora (Makarick et al. 2003). Species range from high to low potential impact and from high to low feasibility of control (Makarick 1999). Nearly half of the Park's 169 exotic plant species have a high potential impact, but only eight of these also have a high feasibility for control (Makarick et al. 2003). In addition, four exotic mammal and six exotic bird species reside primarily in the uplands (forested areas) of GRCA (Stevens and Ayers 2002). The majority of these inhabit developed areas. In BAND, exotics make up approximately 20% of the flora (Allen 1989).

Air Pollution

Relatively little research has been done on the effects of air pollution on the montane and subalpine ecosystems of the southern Colorado Plateau. Research on montane and subalpine ecosystems in the West has focused on southern California and, to a lesser degree, California's Sierra Nevada and Colorado's Front Range. Research in the Southwest has focused on southern Arizona, in the vicinity of large urban centers (Graybill and Rose 1992, Fenn et al. 2003a, 2003b).

Three SCPN units with montane/subalpine ecosystems have air quality monitoring locations: GRCA, MEVE, and BAND (NPS 2002). GRCA and MEVE record data on visibility, ozone, and wet and dry deposition, and BAND records only visibility and wet deposition. In addition, dendrochronological methods have been used to examine tree growth patterns for possible effects of air pollution near Arizona's Mogollon Rim on the southern edge of the Colorado Plateau (Graybill and Rose 1992).

The air pollutants of greatest concern are ozone, sulfate, and nitrogen-based compounds such as nitrate and ammonium/ammonia (NPS 2002). Ozone causes foliar injury and reduced growth. Sulfate is a major component of acid precipitation and impaired visibility. Nitrogen may elevate ozone, be a major component of acid precipitation, impair visibility, increase greenhouse gas emissions, and alter the composition and function of some ecosystems.

The primary sources of the air pollutants affecting forests in Arizona are large point sources (Böhm 1992). More specifically, evidence suggests that the major sources of air pollutants in northern Arizona (including GRCA) are southern California and central Arizona (Vasconcelos 1995, Schreiber 1996). Visitors to SCPN units presumably also contribute to air pollution through their use of motor vehicles, but this is unstudied.

Crown injury linked to air pollution has been reported for ponderosa pine in the mountains of southern California since the 1950s (Arbaugh et al. 1999) and is well-documented today (cf. Miller and McBride 1999). Relatively few reports of such air pollution effects exist for the Southwest. Miller (1989) concluded that some Arizona forests with repeated exposure to ozone and acid deposition had reduced health as a result of the interaction of increased levels of air pollution, pests, and other stressors. Graybill and Rose (1992) found that in extreme cases (six sites in southern Arizona, one on the Mogollon Rim) recent growth patterns of some ponderosa pines indicated that death was imminent. Dendrochronological study of less extreme cases also suggested declines in growth, but linkage to air pollution was less clear. Binkley et al. (1992) postulated that stand- and ecosystem-level effects included reduced growth rates that affect patterns of tree mortality and regeneration, and thereby species composition and vegetation dynamics. Mortality may not be caused directly, but be facilitated by interactions between air pollution and pests and pathogens (see also Takemoto et al. 2001). In addition, some effects may be indirect through modification of environmental factors.

Ozone

As one of the most phytotoxic air pollutants (NPS 2002, Fenn et al. 2003a), ozone has the potential to be a primary anthropogenic stressor for SCPN montane ecosystems. In addition to foliar injury and growth reductions, ozone can combine with other air pollutants, pests, pathogens, moisture stress, and other stressors to have even greater impact. Ozone damage has been reported for forests in southern Arizona (Miller et al. 1995), but much greater damage occurs in California where low elevation montane forests are undergoing a shift in dominance from pollution-susceptible species such as ponderosa pine to ozone-tolerant species (Miller et al. 1997, Takemoto et al. 2001), but this vegetation dynamic has been affected by fire exclusion as well.

Using the SUM06 statistic (the sum of hourly average ozone concentrations ≥ 0.06 ppm) calculated over a three-month period as a measure of ozone levels, a value of 8-12 ppm-hrs is a threshold of foliar damage and 10-15 ppm-hrs is a threshold of growth effects on seedlings (NPS 2002). The maximum SUM06 during 1995-1999 was 31 for GRCA and 19 for MEVE (ozone values are not monitored at BAND) (NPS 2002), well above the thresholds of damage. Moreover, other statistics for ozone (average of the daily 1 hr maximum and annual 4th highest 8 hr average) indicate ozone increased during 1990-1999 in both GRCA and MEVE (NPS 2002).

Nitrogen

The main sources of nitrogen emissions are vehicles, agriculture, power plants, and industry (Fenn 2003b). Although human-caused nitrogen deposition dramatically increased in the United States over the last four decades, the pattern of deposition is highly variable in the western United States, with large areas of low deposition and scattered areas of high deposition downwind from large urban and agricultural areas (Fenn et al. 2003a, 2003b). In SCPN units, BAND reported increased precipitation-weighted mean nitrate ion concentration and nitrate ion wet deposition from 1990 to 1999, while GRCA showed decreases in both and MEVE had mixed results (increases in the former and decreases in the latter).

Negative effects of human-caused nitrogen deposition have not been reported for SCPN units or other areas of the southern Colorado Plateau; however, such effects have been documented elsewhere in the western United States and therefore are briefly reviewed here (for more detail, see Fenn et al. (2003a, 2003b) and Galloway et al. (2003).

Many ecosystems in the western United States are nitrogen-limited, including some forests, shrublands, and grasslands. Nitrogen deposition, therefore, is likely to accelerate growth in these ecosystems. Although this may be viewed as a positive impact for some locations (e.g., commercial forest and agricultural lands), growth may be offset by negative aspects of nitrogen deposition, including ozone enhancement and impacts on sensitive species, some of which appear to respond to even low levels of deposition (Fenn 2003a).

The effects of nitrogen deposition that are well documented for some areas of the western United States include nitrogen enrichment of soils and plants (documented for portions of California), increased flux of nitrogenous trace gases from soil (California and Colorado), decreased diversity of mycorrhizae (Alaska), changed species composition of lichens (Pacific Northwest, California, and Colorado), altered carbon cycling and fuel accumulation in forests (southern California), physiological perturbation of overstory trees (southern California), augmented regional haze (California, Pacific Northwest, and some areas of the Interior West), and precursor to phytotoxic levels of ozone (California) (Fenn 2003a). Although other effects have been proposed, either the evidence is limited or the relationship with nitrogen deposition is unclear.

Other Chemicals

All three SCPN units with air quality monitoring reported improvement in both precipitation-weighted mean sulfate ion concentration and sulfate ion wet deposition from 1990 to 1999 (NPS 2002). State-wide, sulfur dioxide dramatically decreased in Arizona over the previous 20 years (CART 1988).

SCPN Visitation

SCPN visitors have the potential to directly affect montane and subalpine ecosystems primarily as facilitators of the dispersal of exotic species, as possible fire ignition agents, and as additions to regional levels of air pollution (see above). Indirect effects include creating demand for expansion of visitor-use facilities. In limited areas, visitors also alter soil properties through trampling.

NPS Management

The history of NPS management is briefly outlined in *Land-Use History*. Current and future NPS management activities that will affect the montane and subalpine ecosystems of SCPN include maintenance and operational activities, development for visitor-use and administration needs, fire and fuels management, and resources management and restoration. Obviously, the effects of NPS management will be numerous and activity-specific, as well as site-specific.

Ecosystem Descriptions

Ponderosa Pine Forest Ecosystem

Forest ecosystems dominated by ponderosa pine are widespread in the Southwest, covering about 5.6% (34,000 km²) of the combined areas of Arizona and New Mexico (Pase and Brown 1994a). In addition, this is the most widespread forest ecosystem in SCPN.

Much research has been published on the Ponderosa Pine Forest of the Colorado Plateau, as well as elsewhere in the Southwest and the West as a whole. Given the extensive literature and the questionable application of research results from other regions, this report focuses on the literature from the Southwest.

Ecosystem Constraints and Drivers

Topography

Ponderosa Pine Forest occurs at the lowest elevational zone of any montane coniferous forest of the Southwest, approximately 1,850-2,500 m ([Figure 1](#)). The lower, and especially the upper, elevational limits are somewhat obscure. At lower elevations, this forest intergrades with Pinyon-Juniper Woodland. At higher elevations, the forest intergrades with Mixed Conifer Forest, as a gradual transition of species in some areas and as a mosaic of stands in other areas. Where a mosaic transition occurs, stand distribution appears correlated with topography, as stands of Ponderosa Pine Forest occur on drier sites such as south-facing aspects and upper slope positions and stands of Mixed Conifer Forest occur on more mesic sites such as north-facing aspects and lower slope positions.

The transition area with the Mixed Conifer Forest recently has been treated as a separate forest ecosystem in some GRCA reports (cf. Bertolette and Spotskey 2000, Crocker-Bedford et al. 2003), but there is little evidence for or against this status in the literature. In this report, transition stands that have a canopy nearly solely dominated by ponderosa pine are included in the Ponderosa Pine Forest; transition stands with a more diverse canopy are included with the Mixed Conifer Forest.

Climate

Climate data for the Ponderosa Pine Forest are available from several locations within SCPN ([Figure 2](#)), as well as many other locations. In general, the climate is characterized by cool temperatures producing a relatively long (compared to other montane and subalpine ecosystems) potential growing season of 120-180 days (Schubert 1974, Moir 1993, Pase and Brown 1994a). Moisture, not temperature, likely limits plant growth during this period of warm temperatures (Moir 1993).

The climate can be considered borderline for forest, because it is among the driest climates of any forest in North America (Moir 1993, Pase and Brown 1994a). Annual precipitation is in the range of 460 to >760 mm, and at least half comes from monsoonal storms during the growing season (Pase and Brown 1994a). Summer precipitation may be responsible for the existence of this forest in areas that receive less than 640 mm/year (Pase and Brown 1994a). Winters are usually relatively mild compared to other montane and subalpine forest ecosystems, with precipitation falling as snow. Snow cover prevents deep

soil freezing, and snow melt saturates soils (Schubert 1974).

The lower elevation Ponderosa Pine Forest that intergrades with Pinyon-Juniper Woodland has an annual precipitation of 510 mm and an annual temperature of 6°C, while more typical mid-elevation stands average 560-610 mm and 5°C (Moir 1993).

Lightning is a critical component of the climate. A 7756 km² area of mostly Ponderosa Pine Forest in the Jemez Mountains of New Mexico (including BAND) received an average of 2.1 cloud-to-ground lightning strikes/ha annually from 1985 to 1994 (Allen 2002).

Soil

Ponderosa Pine Forest occurs on a wide variety of soils formed from a variety of parent materials (Pase and Brown 1994a), but the soils are generally deep, permeable, and capable of storing snowmelt. The soil moisture regime is ustic, and the soil temperature regime is frigid (Moir 1993).

Soils with Ponderosa Pine Forest in Arizona are Alfisols (Typic Eutroboralfs, Typic Glossoboralfs, and Mollic Eutroboralfs) and Entisols (Typic Cryorthents and Typic Ustorthents) (Hendricks 1985). These soils range from shallow to deep, from fine- to moderately coarse-textured, and are mostly well-drained. Soils with Ponderosa Pine Forest in New Mexico are mostly Alfisols with some Mollisols (Maker and Saugherty 1986).

No detailed historical data are available to document changes in soils of the Ponderosa Pine Forest, but changes can be inferred from studies of the effects of prescribed burning (see next section).

Stand-Scale Disturbance

Fire - The only common stand-scale natural disturbance in Ponderosa Pine Forests of SCPN has been fire. The fire regime in the Southwest has been extensively studied, at least as much as for any forest ecosystem in the world. In short, fire has been a key driver of composition and especially structure of Ponderosa Pine Forests in the Southwest, including the southern Colorado Plateau, for as long as ponderosa pine has dominated landscapes (cf. Weng and Jackson 1999).

The identification of fire as a primary driver of the Ponderosa Pine Forest dates back to over a century ago, when Euro-Americans were surveying the resources of the Southwest; however, at that time cultural biases, which led observers to believe that fires were unnatural and that Native Americans were the primary source of ignitions, precluded a clear understanding of the role of fire in this ecosystem (Allen 2002, Swetnam and Baisan 2003). Scientific understanding of fire in Ponderosa Pine Forests of the Southwest dates at least back to Weaver (1951).

After decades of research, it is abundantly clear that the Ponderosa Pine Forest was formerly characterized by low-intensity surface fires (Swetnam and Baisan 1996, Dahms and Geils 1997), which may have occasionally, and in small areas, crowned via fuel ladders. A review with data for 53 sites in the Southwest dominated or co-dominated by ponderosa pine (including sites transitional with Pinyon-Juniper Woodland and Mixed Conifer Forest) reported mean fire return intervals for the period 1700-1900 were 2-17 years for fires scarring one or more trees and 4-36 years for fires scarring 10 and 25% of scarred trees (part of the range in variation is accounted for by unequal sizes of study sites) (Swetnam and Baisan 1996). However, a critique of the use of fire scars to estimate fire return intervals suggested that return intervals in ponderosa pine forests across the Western United States may be underestimated by an order of magnitude or more (Baker and Ehle 2001).

Fire intervals varied along gradients within the Ponderosa Pine Forest. Longer intervals tend to be associated with sites that are (1) low elevation (apparently because of lower production of fine fuels to carry fires), (2) topographically isolated, (3) higher elevation (apparently because of high moisture levels), and (4) more moist (Allen et al. 1995, Swetnam and Baisan 1996). At the landscape scale, longer fire intervals are related to the amount and horizontal continuity of fuels on the soil surface; therefore, fire frequencies tend to be lower on less productive sites (Rollins et al. 2002).

Fire intervals also varied with climate (e.g., Swetnam and Baisan 1996, Touchan et al. 1996, Fulé et al. 2000). Large fire years are correlated with severe droughts, especially when preceded by one to three years of high precipitation during which fine fuels increased. Small fire years are correlated with high precipitation. Therefore, the impact of episodic climatic events was largely through shifts in the fire regime.

The high-frequency, low-intensity surface fire regime had many effects. Forest structure was kept within a relatively narrow range of variability (in comparison to other montane and subalpine forests). Microsites for tree regeneration were produced as reductions in the herbaceous layer decreased competition for germinating seedlings (Sackett et al. 1996). Cohorts of seedlings and saplings were diminished, but the growth of survivors increased (Dahms and Geils 1997). Fuel loads were kept within a relatively narrow range of variability. In addition, based on studies of prescribed burns in modern forests, soil properties were altered (Bennett 1974). The layer of duff on the soil surface was kept thin and patchy. This enhanced moisture availability (Covington et al. 1997, Feeney et al. 1998). In addition mineralization was increased (White 1986, White 1996), which increased nutrient mobilization (Covington and Sackett 1984) and nutrients on the soil surface (Covington and Sackett 1990), including nitrogen (Harris and Covington 1983, Covington and Sackett 1986, 1990, 1992, Ryan and Covington 1986). Populations of arbuscular mycorrhizae in the soil also may have increased (Korb et al. 2003).

Livestock grazing and active fire exclusion practices abruptly decreased the frequency of surface fires in the late 19th century (see *Overview*). Without surface fires to consume woody fuels and maintain low densities of trees, fuel loads increased and became more continuous both horizontally and vertically. Therefore, today's fires tend to become high-intensity crown fires.

Wind - Although windthrows of single to a few trees occur (Pearson 1950), especially with the coarsely textured soils of the North Rim region of GRCA (Fulé et al. 2002a), there is little in the scientific literature about stand-scale effects of wind on Ponderosa Pine Forest.

Pests and Pathogens - Bark beetle outbreaks in BAND in 1955-1958 (Allen 1989) and in many areas of the southern Colorado Plateau in 2002-2003 (personal observation) indicate that, at least under certain conditions, bark beetles can be a stand-scale agent of disturbance, even resulting in a shift of the ecotone between Ponderosa Pine Forest and Pinyon-Juniper Woodland upslope 1-3 km upslope between (Allen 1989).

Research in northern Arizona indicates a guild of bark beetles in the Ponderosa Pine Forest (Sánchez-Martínez and Wagner 2002). The guild consists of seven species: *Dendroctonus frontalis*, *D. brevicomis*, *D. valens*, *D. approximatus*, *D. ponderosae*, *Ips pini*, and an unidentified species of *Ips*. It appears that populations of these beetle species are maintained in forests, possibly in lightning-scarred trees.

At least the more aggressive beetle species infest scattered, small clusters of one to ten trees, but larger outbreaks have occurred, especially frequently on the northern Kaibab Plateau (cf. Douglas and Stevens 1979). Data from Lang and Stewart (1910 in Pollock and Suckling 1997) indicate that insects were a major cause of mortality on the Kaibab Plateau, with some townships having >10% of merchantable trees (including ponderosa pines > 46cm) killed by insects. One of the aggressive species of bark beetles, *Dendroctonus brevicomis*, appears to prefer larger, more mature trees of 60-81 cm dbh and 150-300 years age (Miller and Keen 1960). The pattern of attack on Ponderosa Pine Forests of the Colorado Plateau may differ from other areas (Sánchez-Martínez and Wagner 2002).

Recent evidence does not support the assumption that high tree densities enhance the probability of large outbreaks of bark beetles (Sánchez-Martínez and Wagner 2002). However, tree mortality from bark beetles in BAND in 1955-1958 and in the southern Colorado Plateau in 2002-2003 suggests that trees are more susceptible during drought years, especially on slope aspects, slope inclinations, and soils where moisture stress levels are highest.

Other insects that may impact southwestern Ponderosa Pine Forests include pine sawflies (*Neodiprion* spp.) (McMillin and Wagner 1993), but little information is available on this pest in the Southwest.

Pandora moth (*Coloradia pandora*), which causes defoliation of ponderosa pine at the landscape scale on the southern Colorado Plateau, does not appear to significantly impact tree growth and vigor (Miller and Wagner 1989).

Southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) is another pest on ponderosa pine. Prior to Euro-American influence, southwestern dwarf mistletoe likely occurred throughout forests and had a distribution similar to its current distribution, but its abundance may have been lower (Dahms and Geils 1997).

Other Animals - Elk and deer are the major large ungulates in Ponderosa Pine Forests of the Southwest (Dahms and Geils 1997). Animal population dynamics prior to Euro-American influence are unknown, but elk and deer likely affected tree regeneration patterns. For example, regeneration of quaking aspen, a heavily browsed species, would have been reduced during periods of high elk and deer populations.

Interactions Among Disturbance Agents - Other than fire enhancing elk and deer browse, only one significant interaction among the above disturbance agents, at least for old-growth stands of Ponderosa Pine Forest, has been noted in the literature. Southwestern dwarf mistletoe can form dense "witches brooms" on trees, and these clusters of branches and foliage can be a fuel ladder for fire to enter the canopy, possibly even resulting in crown fires (Alexander and Hawksworth 1975). Even where fire doesn't crown but remains on the surface, mistletoe can increase tree mortality in fires (Roth 1974, Harrington and Hawksworth 1990).

Unreported but likely interactions include the facilitation of spot crowning of surface fires in areas of small clusters of trees killed by bark beetles. In addition, high population densities of elk and deer likely reduced the frequency of surface fires by decreasing the abundance and spatial continuity of grasses and other herbs that fuel surface fires.

Vegetation Dynamics

If succession is to be recognized as a process in southwestern Ponderosa Pine Forest before Euro-American influence, it is best considered on an individual-tree scale, rather than a stand or landscape scale, because large-scale, intensive disturbances appear to have been uncommon.

Succession at the individual-tree scale began with the death of a large tree (Pollock and Suckling 1997, see also Cooper 1960, White 1985). When fire consumed the dead tree, it created a microsite that was nutrient rich and free from plants, i.e., a potential site of ponderosa regeneration. During periods when seed availability and climate conditions were conducive to ponderosa pine regeneration, seedlings established (otherwise, the microsite would be re-colonized by grasses and other understory plants). Whatever seedlings survived for a few years would eventually be exposed to surface fires. Clusters of even-aged saplings would be thinned by surface fires, leaving few if any trees to enter the subcanopy and canopy. Thereby, succession at this scale, when scattered throughout stands, produced an uneven-aged, dynamic, relatively stable forest.

Although the change in fire regimes from surface to crown fires has resulted in stand- and landscape-scale succession, surprisingly little has been written about such succession following crown fires in old-growth Ponderosa Pine Forests. Some detail is available from New Mexico (Moir 1993) (although it is unclear whether the descriptions are for old- or second-growth stands). Succession in mid-elevation ponderosa pine-Gambel oak includes a long period of dominance by oak and New Mexico locust (*Robinia neomexicana*) before overtopping by ponderosa pine (see also Harper et al. 1985). At lower elevations with ponderosa pine, pinyon pine (*Pinus edulis*), and gambel oak, succession involves prolonged dominance by gambel oak and/or junipers (*Juniperus* spp.). Near the low elevation limit for Ponderosa Pine Forest, it can be replaced by Pinyon-Juniper Woodland either as a prolonged seral stage or possibly as a permanent replacement.

Composition and Structure

Trees

Before Euro-American Influence - The canopy of most of the Ponderosa Pine Forest had been nearly a

monoculture of ponderosa pine whose crown cover is estimated to have ranged from 17 to 33% (Pearson 1923, 1950, White 1985, Covington and Sackett 1986). Stands at higher elevation near the transition with Mixed Conifer Forest may have had scattered individuals of at least white fir, Douglas fir, and quaking aspen, with quaking aspen more common in areas where surface fires had crowned.

Understory layers of the Ponderosa Pine Forest were more diverse than the canopy. In low elevation stands, pinyon pine was abundant in the interspaces between canopy ponderosa pines, reflecting a transition with Pinyon-Juniper Woodland. Gambel oak and New Mexico locust also occurred in low elevation stands and, unlike pinyon pine, extended into mid-elevation sites. Seedling and sapling ponderosa pines occurred throughout the range of the forest, but shared the understory with young white fir and Douglas fir at higher elevations.

The structure of stands prior to Euro-American impact has been repeatedly described as "open and park-like", with widely spaced tall trees and a dense herbaceous layer dominated by grasses -- more woodland than forest. This conclusion is often justified by reference to early Euro-American explorers of the Southwest who left accounts such as

The ground was covered with fresh grass and well timbered with tall pines... (Sitgreaves 1853)

We came to a glorious forest of lofty pines...every foot being covered with the finest grass, and beautiful broad grassy vales extended in every direction. The forest was perfectly open... (Beale 1858)

Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade. The ground is unobstructed and inviting. (Dutton 1882)

...where the pines predominate the forest is very open. (Dutton 1882)

There is even a quantitative description:

[Our route] is beneath the pines standing at intervals varying from 50 to 100 feet... (Dutton 1882)

Modern studies from areas where fire has not been excluded generally support such descriptions (cf. Madany and West 1983, Fulé and Covington 1995).

The "open and park-like" paradigm, which dates at least to Weaver (1951), has been challenged. Pollock and Suckling (1997), in a report that appears not to have been peer-reviewed within the scientific community, noted that Beale's (1858) oft-quoted remarks were describing a low-elevation area of transition between Pinyon-Juniper Woodland and Ponderosa Pine Forest. Further, they reported that Beale's journal referred to dense, heavy, or heavily timbered forests three times as frequently as open forests. In addition, Baker and Ehle (2001) have challenged the high frequency of surface fires, arguing that fire return intervals in ponderosa pine forests across the Western United States may be underestimated by an order of magnitude or more, thus making greater landscape heterogeneity likely.

Perhaps there was a greater range of forest densities than indicated by 19th century travelers. Woolsey (1911) wrote, "An accurate picture of the pre- [Euro-American] settlement ponderosa pine forest would most likely describe a mosaic not only with an open, grass savanna and clumps of large, yellow-bark ponderosa pine, but also with a few dense patches and stringers of small, blackjack [young ponderosa] pines." Although Woolsey's (1911) observations occurred a few decades after Euro-American influence began, it is likely that variations in fire frequency, especially as related to topographic features (Allen et al. 1995, Swetnam and Baisan 1996), resulted in differences in structure among stands prior to Euro-American influence. Therefore, while open, park-like conditions may have been common, likely too were sites where trees were more dense, giving the forest a less uniform, somewhat more patchy appearance

Tree densities and basal areas of Ponderosa Pine forest unaltered or relatively unaltered by Euro-

Americans have been estimated by use of forest survey data collected in the early 20th century, by reconstruction based on current forest trees and snags, and by projections based on more recent trajectories of change. The following examples are for three estimations from the GRCA region:

1. Survey data from 1910 for the Kaibab Plateau indicate a mean density of 112 trees/ha (for trees >15 cm dbh) and 264 trees/ha (for trees <15 cm dbh) (Garrett et al. 1997).
2. Reconstruction data for three sites of relatively unaltered Ponderosa Pine Forest in the North Rim portion of GRCA suggest mean densities of 153-160 trees/ha and mean basal areas of 17-21 m²/ha (for trees >2.5 cm dbh) (Fulé et al. 2002a). However, values ranged widely: densities of 20-646 trees/ha and basal areas of 4-77 m²/ha.
3. Trajectories determined since 1935 for GRCA (South and North Rims) include a decline in basal area from 42 to 28 m²/ha (for trees >10 cm dbh). It is likely that basal area only slightly increased from 1880 to 1935 (Crocker-Bedford et al. 2003).

These wide differences in estimates are in part the result of different dbh limits, but they also suggest that each method of estimating the structure of past forests has limitations.

Yet another possibility for estimating forest structure in the GRCA region appears not to have been reported in the literature. Dutton's (1882) description of trees being 15.2 to 30.4 m apart can be used as an estimate of mean distance among trees. Therefore, tree density nearly immediately after the fire regime had changed was 11-43 trees/ha. Although Dutton (1882) did not specify the size of trees being described, he likely was describing canopy and possibly near-canopy size trees.

More generally, Pollock and Suckling (1997) estimated that typical stand densities in the Southwest, depending on soil type, were 12-37 trees/ha for trees >48 cm dbh, 25-74 trees/ha for trees >30 cm dbh, and 250-500 trees/ha for all trees (lower dbh limit undefined).

The life history of ponderosa pine has also received much attention. As early as 1931, it was recognized that ponderosa pine rarely regenerates, but produces large numbers of seedlings when it does regenerate (Pearson 1931). Regeneration requires high moisture and an absence of fire (Dahms and Geils 1997); presumably also heavy seed years. Early studies suggested that clusters of seedlings and saplings are even-aged (Cooper 1960, 1961), but more recent research indicated that clusters are mixed-age (and consist of 3-44 trees in clusters covering 200-2,900 m²) (White 1985).

Examination of ages of contemporary trees pre-dating the influence of Euro-Americans supports the finding that regeneration was uncommon (White 1985). Also, regeneration has been multi-modal with broad periods of greater establishment (Mast et al. 1999). Surprisingly, no clear relationship between regeneration of these older trees and either fire or climate was evident, -perhaps because so few trees survived the surface fires that thinned (or eliminated) individual clusters.

Most mortality of seedlings and saplings presumably was caused by reoccurring surface fires. Mortality of larger trees was caused by wind, lightning, mistletoe, and bark beetles (Pearson 1950), as well as senescence (Dahms and Geils 1997). Mortality measured from 1925 to 1940 indicated that of the total mortality of 0.33% for trees >30 cm dbh, bark beetles accounted for 33%, lightning for 31%, wind for 20%, and mistletoe for 6%, leaving 10% for other reasons including root pathogens (Pearson 1950).

With Euro-American Influence - The reduced fire frequencies accompanying livestock grazing and, later, active fire exclusion have dramatically changed the structure of most areas of Ponderosa Pine Forest in the Southwest (Weaver 1951, Harrington and Sackett 1990, Covington and Moore 1994a, 1994b, Dahms and Geils 1997), greatly homogenizing stands and landscapes (cf. Allen et al. 2002). For GRCA, Fulé et al. (2002a) compared livestock grazing, wildlife grazing, fire exclusion, tree cutting, and climate fluctuations and concluded that changed forest structure was the result primarily of the changed fire regime. In other areas, however, climate appears to have been more important. For example, although the fire regime changed in the Chuska Mountains of Arizona and New Mexico when livestock grazing was

initiated (in about 1830), forest structure didn't change until the early 20th century, when warm, wet weather on the Colorado Plateau apparently enabled tree regeneration (Savage 1991). Many but not all areas of the southern Colorado Plateau experienced a burst of regeneration in 1919 (Moir 1993) that has been correlated with uncommon seasonal and interannual climatic factors, along with anthropogenic disturbances (Savage et al. 1996).

There are many different facets to the changes in forest structure, including changes in forest densities, distribution of diameter classes, structural diversity, and tree vigor. Most research has focused on the change in forest densities -- it is the most visually obvious change and, perhaps, the one most amenable to attempts to quantify. Considering the data for GRCA given above, the changes calculated for mean density and basal area from pre-livestock grazing to recently are:

1. Survey data from 1910 for the Kaibab Plateau (Garrett et al. 1997) density increased 154% for trees >15 cm dbh (112 to 284 trees/ha) and >742% for trees <15 cm dbh (264 to >2224 trees/ha)
2. Reconstruction data for North Rim of GRCA (Fulé et al. 2002a) density increased 154-485% for trees >2.5 cm dbh (153-160 to 389-936 trees/ha) basal area increased 44-59% for trees >2.5 cm dbh (17-21 to 26-31 m²/ha)
3. Projections based on trajectories for the North and South Rims of GRCA (Crocker-Bedford et al. 2003) basal area decreased 33% for trees >10 cm dbh (42 to 28 m²/ha)

The third data set shows atypical results, as most studies indicate increases in density (Dahms and Geils 1997) if not in basal area also. However, in addition to being collected from somewhat different areas (which can affect the magnitude of structural changes; Menzel and Covington 1997), the tree data sets cover different ranges of diameter classes. When changes are examined by diameter classes, it is clear that the greater increase in density occurred within the smaller size classes (Dahms and Geils 1997).

The increased density of smaller diameter trees skewed size class distributions toward smaller trees (Dahms and Geils 1997). It also likely decreased structural diversity within stands (Dahms and Geils 1997), as formerly open spaces between patches filled in with tree regeneration.

The increased density of small trees decreased overall tree vigor. With increased shade and root competition, as well as less available moisture and nutrients, tree growth rates declined in all size classes (Clary and Ffolliott 1969 in Harrington and Sackett 1990). It appears that reduced vigor has been especially damaging to older, larger trees. This was predicted by Gus Pearson (in Fulé et al. 2001) who wrote in 1944,

Now that reproduction has come in, young trees will claim an ever increasing share of the meager moisture supply which the veterans were able to monopolize as long as fire and grazing prevented regeneration. It is expected that another 20 years will witness a marked decline in the growth of large trees.

Data suggest that competition from smaller, younger trees has indeed reduced the vigor of larger, older trees present before Euro-American influences (Feeney et al. 1998; see also Graybill and Rose 1992). The reduced vigor apparently has increased mortality rates for large, old trees. Reported losses in large size classes since the beginning of Euro-American influence are in the range of 34-51% (Dahms and Geils 1997, Garrett and Soulen 1997, Crocker-Bedford et al. 2003). Elevated mortality rates in GRCA are related to today's older trees being more susceptible to pathogens, drought, and injury related to increased stress through increased competition (Kaufmann and Covington 2001).

In contrast to forest tree structure, changes in tree composition have been relatively minor, at least in most elevations. Forest reconstructions for the southern Colorado Plateau suggested shifts in species composition toward less ponderosa pine and (a) more gambel oak in WACA (Menzel and Covington 1997), (b) more gambel oak, white fir, and Douglas fir in an area west of Flagstaff, Arizona (Fulé et al. 1997), and (c) more gambel oak, New Mexico locust, and pinyon pine on the North Rim of GRCA (Fulé et

al. 2002a); however, methods of forest reconstructions may be biased toward change in shorter-lived species and individuals.

Changes in forest composition would seem to be especially likely in higher elevation stands, near the transition with Mixed Conifer Forest. These mesic stands would be especially subject to increasing forest density, especially with their proximity to seed sources of shade-tolerant, fire-sensitive conifers such as white fir.

Shrubs and Herbs

Before Euro-American Influence - Only generalized qualitative descriptions are available for the understory of the Ponderosa Pine Forest before or near the beginning of Euro-American influence, such as

The ground was covered with fresh grass...(Sitgreaves 1853)

...every foot being covered with the finest grass... (Beale 1858)

Such early descriptions, as well as contemporary stands that are relatively undisturbed, indicate that few shrub species occurred in the undisturbed Ponderosa Pine Forests of the Southwest, and what shrubs were present were rarely abundant (Mead 1930, Madany and West 1983, Pase and Brown 1994a). In addition, the herb layer was likely dense and usually dominated by graminoids (Moir 1993, Pase and Brown 1994a).

With Euro-American Influence - With little knowledge of former conditions, most descriptions of changes in shrubs and herbs with Euro-American influence refer to generalized qualitative changes related to increases in forest density and duff thickness (cf. Arnold 1950, Pase and Brown 1994a, Dahms and Geils 1997). One approach to understanding the changes is through inference from results of prescribed burning.

Little mention is made of the response of shrub cover to prescribed burning; however, some evidence suggests that the shrub understory decreased slightly during the period of Euro-American influence (cf. Covington et al. 1997). In contrast, comparison of an open shrub layer in a forest with a relatively uninterrupted fire regime with the dense shrub layer of a nearby grazed, unburned forest indicates that shrub cover, at least in some areas, has increased (Madany and West 1983).

Results from prescribed burning (often coupled with tree thinning) support the general consensus that the herb understory became less abundant with Euro-American influence (cf. Covington et al. 1997). Research in GRCA indicated that a site where the surface fire regime had been more interrupted had lower species richness but greater cover of exotic species than sites more frequently burned (Springer et al. 2000). Total plant cover ranged from about 18% in an area without fire to 30-45% in areas where the fire regime had changed less.

More detailed information, including species lists, is available (cf. Moir 1993, Pase and Brown 1994a, Springer et al. 2000).

Animals

The New Mexico Department of Fish and Game maintains a searchable website (<http://nmnhp.unm.edu/bisonm/bisonquery.php>) which lists animal taxa for Ponderosa Pine Forest in New Mexico and Arizona. Currently, the site lists 32 molluscs, 5 amphibians, 15 reptiles, 132 birds, and 156 mammals, more in each category than any other ecosystem considered in this report (except more reptiles are reported for the Montane Shrubland). Of course many of the taxa listed have ranges that extend outside the Ponderosa Pine Forest.

Little information is available on the history of most species (Dahms and Geils 1997), but the New Mexico Department of Fish and Game considers some of the taxa listed on their website as extirpated and extinct. All six extirpated species and the one extinct species of the Ponderosa Pine Forest are

mammals.

Anthropogenic Stressors

The major anthropogenic stressors affecting or potentially affecting the Ponderosa Pine Forest of SCPN are fire exclusion, exotic species, and air pollution.

The impact of fire exclusion on soils, vegetation dynamics, and ecosystem structure and composition is covered above.

Few data are available on exotic species. In GRCA Ponderosa Pine Forests, exotics account for 2-21% of plant ground cover (Springer et al. 2000). The percentage is 2 and 3% in sites with a relatively uninterrupted fire regime on the North Rim, 4 and 9% in drier, more disturbed South Rim sites, and 21% in a site where the fire regime had been more interrupted. Species were smooth brome (*Bromus inermis*), cheat grass (*Bromus tectorum*), bur buttercup (*Ceratocephala testiculata*), redstem filaree (*Erodium cicutarium*), sweet clover (*Melilotus* sp.), Kentucky bluegrass (*Poa pratensis*), dandelion (*Taraxacum officinale*), goatsbeard (*Tragopogon dubius*), white clover (*Trifolium repens*), and common mullein (*Verbascum thapsus*).

Little is known about air pollution effects on the Ponderosa Pine Forest of the Southwest. Ozone levels at the south rim of GRCA, measured by the ozone SUM 06 statistic, reached 27 ppm-hrs in 1996, 28 ppm-hrs in 1998, and 31 ppm-hrs in 1999 (Bowman 2003). Foliar injury on ponderosa pines was 15-50% at 25-30 ppm-hrs in Lassen Volcanic, Sequoia/Kings Canyon, and Yosemite National Parks in California (NPS 2002). This suggests that ozone may be impacting the Ponderosa Pine Forest in GRCA and possibly other SCPN units.

Figure 3. Ecosystem characterization model of Ponderosa Pine Forest. Symbols are as follows: rectangles = biotic components, ovals = interactive controls, solid rounded rectangles = state factors, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships. Numbers next to relationships are keyed to [Table 1](#)

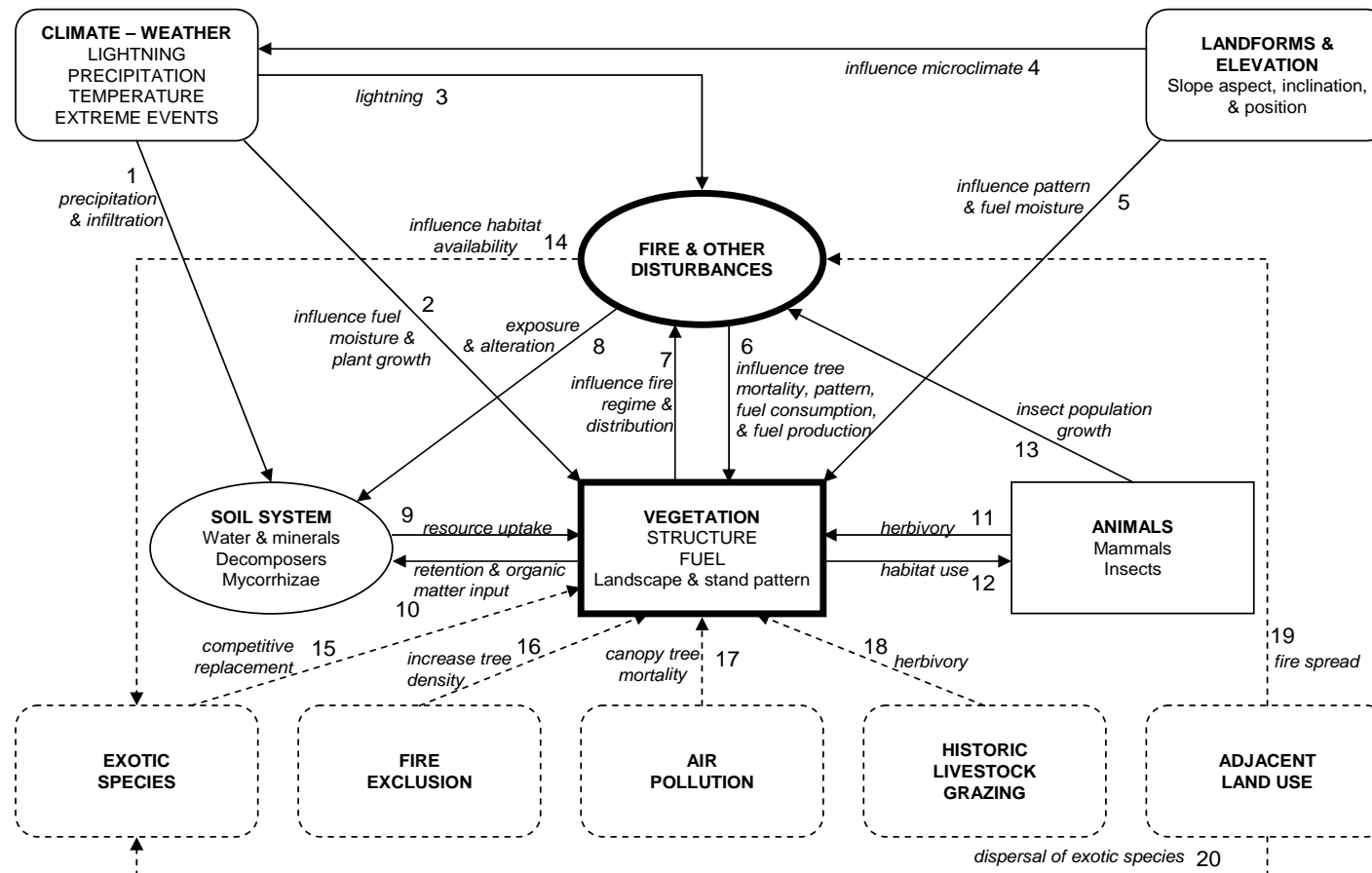


Table 1. Explanation of relationships shown in ecosystem characterization model of Ponderosa Pine Forest. Numbers for relationships are keyed to [Figure 3](#).

Relationships	Circa 1880	Today
1	Precipitation and infiltration add to soil moisture. Snowmelt of winter snowpack is critical in recharging soil moisture (see text for details).	Same, but in addition, infiltration of summer monsoonal rain and, to a lesser degree, winter snowmelt is reduced by thick layer of duff.
2	Climate largely determines moisture level of fuel, is a major factor determining plant growth, and influences tree regeneration	Same
3	Lightnin ignites fires	Same
4	Landforms, especially slope & aspect, result in microclimatic variation. Elevation affects precipitation and evapotranspiration.	Same, except that in some areas, denser tree cover reduces microclimatic variation on the soil surface
5	Variation in landforms contributes to heterogeneous vegetation pattern in which tree densities differ among and within stands and affects fuel moisture. Elevational differences also affect species composition.	Same; however, impact of landform variation on microclimate is reduced in areas with denser tree cover
6	Surface fires thin patches of tree regeneration (see text for details). Pine bark beetle infestations kill scattered, larger trees. Heterogeneous surface fire pattern contributes to heterogeneous vegetation pattern. Fuels are consumed by frequent surface fires, precluding buildup of fuels between fires (see text for details). Pine bark beetle infestations occasionally produce coarse fuels.	Crown fires kill trees in all size classes. Pine bark beetle infestations kill scattered, larger trees. In areas with crown fire regime, more homogeneous fire pattern reinforces a more homogeneous vegetation pattern. Fuels build up between infrequent crown fires and are mostly consumed in fires (see text for details). Pine bark beetle infestations occasionally produce coarse fuels.
7	Light fuel load; horizontally continuous, annually regenerated fine fuel on forest floor; and vertically discontinuous fuel result in fire regime of frequent, low intensity surface fires (see text for details). Heterogeneous vegetation pattern combines with surface fire regime to produce a heterogeneous fire pattern.	Heavier fuel load and vertically continuous fuel result in fire regime of infrequent, high intensity crown fires (see text for details). In areas with more homogeneous vegetation pattern and high fuels, crown fire regime produces a homogeneous fire pattern.
8	Surface fires partially and patchily expose soil surface	Crown fires expose soil surface and alter soil properties
9	Water and minerals in soil are absorbed by plants	Same, but water and minerals may be less available
10	Plants stabilize soil and produce coarse woody debris and litter	Same
11	Herbivores graze vegetation. Unusually high deer populations can reduce the herb layer	Same
12	Vegetation serves as habitat for animals	Same, but habitat is different
13	Population growth of pine bark beetles leads to insect infestations.	Same
14	Not applicable	Disturbance inside SCPN units creates habitat for exotic species.
15	Not applicable	Exotic species successfully compete with native species. Some exotics may have the potential to alter ecosystem processes
16	Not applicable	Fire exclusion by NPS results in increased tree density
17	Not applicable	Ozone and other air pollutants may increase the mortality of canopy trees
18	Not applicable	Livestock grazing removed fine fuels (by consuming herbaceous plants) and likely changed species composition.
19	Not applicable	Human-caused fires originating outside SCPN units may spread into units.
20	Not applicable	Disturbances in lands adjacent to SCPN units provide habitat for establishment of exotic species, which are then more likely to be dispersed into the units.

Figure 4. Ecosystem dynamics model of Ponderosa Pine Forest. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model (Figure 3) by showing the various communities (within different states) and processes that form them. Numbers next to relationships and letters next to transitions are keyed to Table 2.

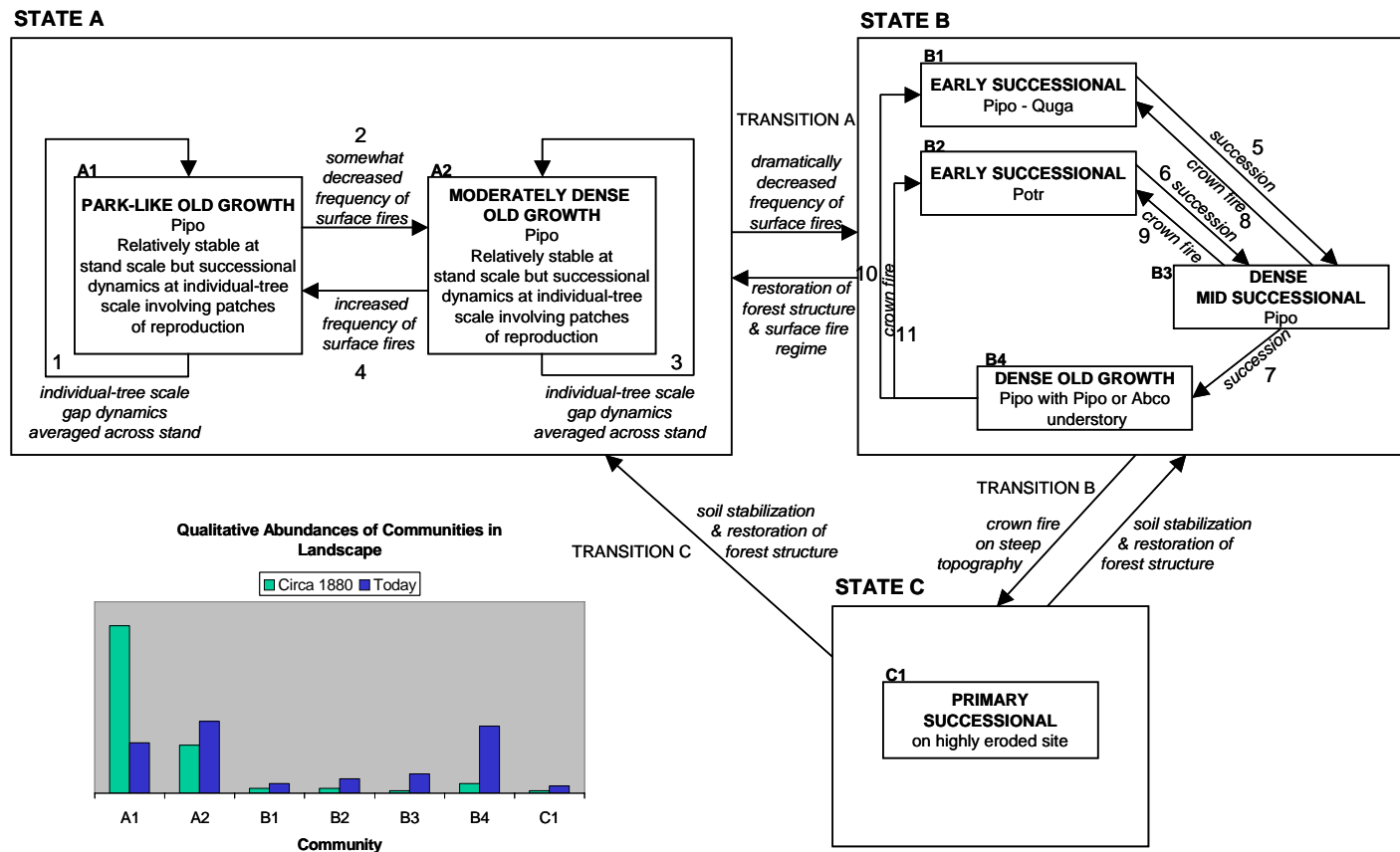
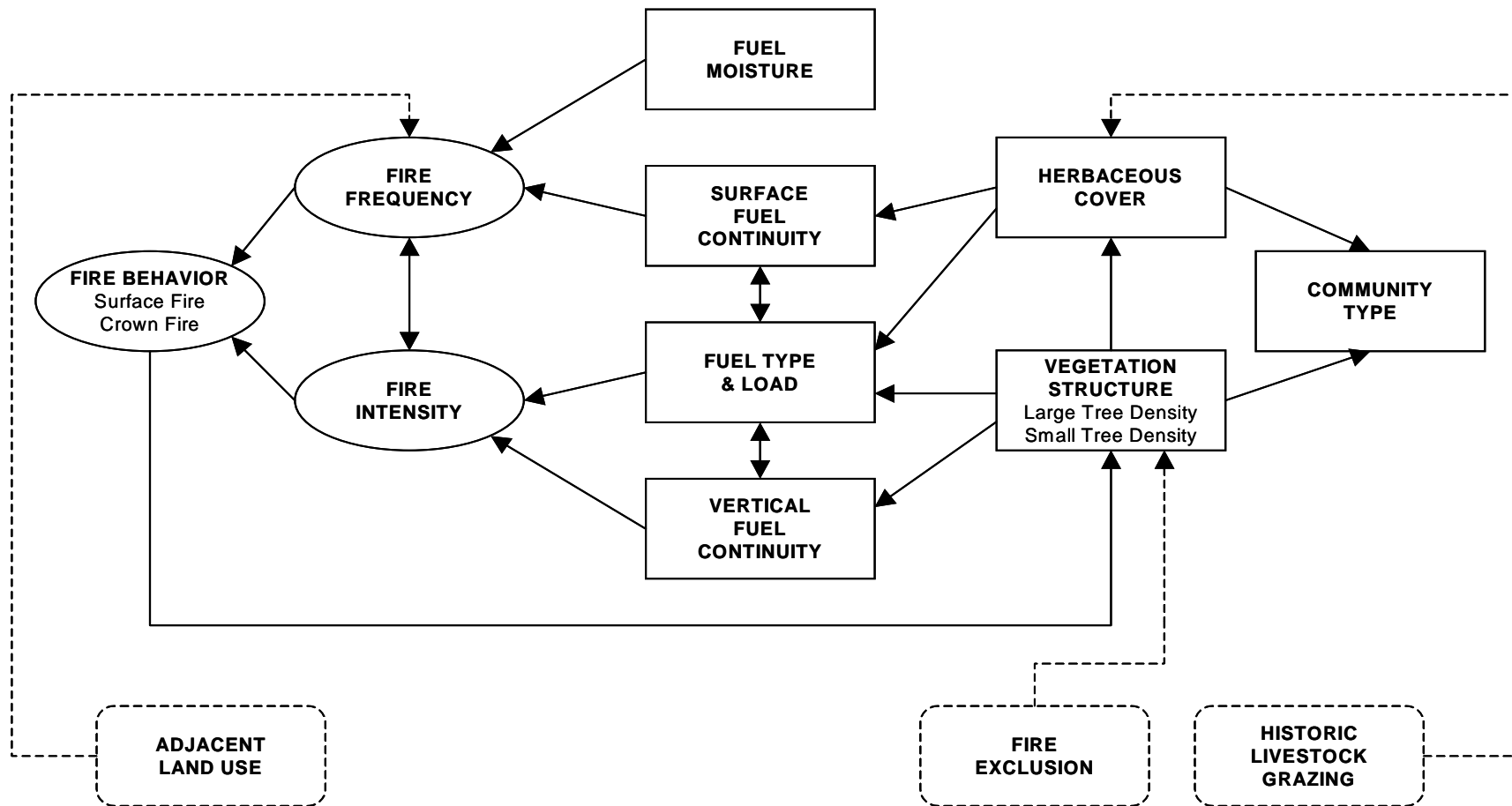


Table 2. Explanation of relationships and transitions shown in ecosystem dynamics model of Ponderosa Pine Forest. Numbers for relationships and letters for transitions are keyed to [Figure 4](#).

Relationships and Transitions	Circa 1880	Today
1	Treefalls of single to a few trees, followed by surface fire, result in regeneration of trees that, after thinning by additional surface fires, replace the original canopy tree(s) (see text for details).	Same, at least in sites with low tree density.
2	A relatively small decrease in fire frequency induced by climate leads to an increase in stand density.	Same, at least in sites with low tree density.
3	Treefalls of single to a few trees, followed by surface fire, result in regeneration of trees that, after thinning by additional surface fires, replace the original canopy tree(s) (see text for details).	Same, at least in sites with moderate tree density.
4	A relatively small increase in fire frequency induced by climate leads to a decrease in stand density.	Same, at least in sites with moderate tree density.
5	Uncommon.	Succession results in suppression of gambel oak.
6	Uncommon.	Uncommon, but where it occurs, succession results in suppression of quaking aspen.
7	Uncommon.	Succession leads to old-growth characteristics, often with an understory of white fir.
8	Uncommon.	Crown fire replaces mid successional stand, in which quaking aspen was absent, with early successional stand.
9	Uncommon.	Crown fire replaces mid successional stand, in which quaking aspen was present, with early successional stand.
10	Uncommon.	Crown fire replaces old growth in which quaking aspen was absent (often low- to mid-elevation sites), leading to the establishment of an early successional stand dominated by ponderosa pine and gambel oak.

Relationships and Transitions	Circa 1880	Today
11	Uncommon.	Crown fire replaces old growth in which quaking aspen was present (often high-elevation sites). Root sprouting leads to establishment of an early successional stand dominated by quaking aspen.
A	Uncommon.	Fire exclusion takes stands from State A to State B (see text for details). Reversion to State A requires restoration of forest structure and surface fire regime.
B	Uncommon.	Crown fire on steep topography may be followed by severe soil erosion, taking stands from State B to State C. Reversion to State B requires soil stabilization and restoration of forest structure.
C	Uncommon.	Transition to State A requires soil stabilization and restoration of forest structure.

Figure 5. Mechanistic model of Ponderosa Pine Forest. This model provides more detail on the mechanisms involved in the vegetation - fuel - fire interaction of the ecosystem dynamics model (Figure 4). Symbols are as follows: rectangles = biotic components, ovals = interactive controls, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships.



Mixed Conifer Forest Ecosystem

Forest ecosystems dominated by various combinations of ponderosa pine, white fir, Douglas fir, blue spruce, quaking aspen, Engelmann spruce, subalpine fir, and others are neither common nor rare in the Southwest. Mixed Conifer Forest covers 10,117 km² in the Southwest (Gottfried 1978), including approximately 3% of Arizona and 4% of New Mexico (Moir and Ludwig 1979), but its area may be increasing (Heinlein 1996, Dahms and Geils 1997), presumably as a result of fire exclusion (see below). Stands of Mixed Conifer Forest occur in on a few SCPN units, but and scattered trees suggestive of this forest ecosystem occur in several other SCPN units.

A moderate amount of research has been done on the Mixed Conifer Forest of the southern Colorado Plateau. Although other authors have freely utilized literature from mixed conifer forests of the Sierra Nevada and elsewhere, the application of that research to the southern Colorado Plateau appears at least questionable. Therefore, this review focuses on literature from the Southwest.

Ecosystem Constraints and Drivers

Topography

Mixed Conifer Forest occurs in the middle elevations of the coniferous forest zone of the Southwest, from approximately 2,450 to 2,900 m (Pase and Brown 1994a). Unlike the Ponderosa Pine Forest, Mixed Conifer Forest does not occupy large contiguous areas but rather occurs in smaller, discontinuous areas surrounded by Ponderosa Pine Forest at lower elevations.

Throughout much of its elevational range, the Mixed Conifer Forest consists of a mosaic of forest patches of varying species composition (White and Vankat 1993). This mosaic and an overlap of dominant species such as ponderosa pine with the Ponderosa Pine Forest and Engelmann spruce and subalpine fir with the Spruce-Fir Forest result in lower and upper elevational boundaries that can be obscure.

At lower elevations, the mosaic consists of patches of mixed composition (but usually including ponderosa pine) on more mesic sites such as north and east aspects and lower slope positions, and patches of nearly pure ponderosa pine occur on more xeric slopes such as south and west aspects and higher slope positions. As described in the *Ponderosa Pine Forest*, this transition area recently has been treated as a separate forest ecosystem in some GRCA reports (cf. Bertolette and Spotsky 2000, Crocker-Bedford et al. 2003). However, because there is little evidence for or against this status in the literature, in this report transition stands are treated as either Ponderosa Pine Forest or Mixed Conifer Forest, depending on canopy composition.

At mid-elevations, the mosaic of the Mixed Conifer Forest consists of stands with varying species dominance depending on a topographic-moisture gradient (White and Vankat 1993). At high elevations, the mosaic consists of stands of mixed dominance on more xeric sites and stands dominated by Engelmann spruce and subalpine fir on more mesic sites.

Super-imposed on the topographically based mosaic is another mosaic based on disturbance, in which quaking aspen may dominate recently disturbed sites, especially in more mesic sites.

Climate

Climate data collected in the Mixed Conifer Forest are uncommon. In general, the climate is characterized by cool to cold temperatures producing a short to moderately long growing season of 90-120 days. Unlike in the Ponderosa Pine Forest, moisture is usually not limiting during the growing season because precipitation is ample (Moir 1993). Combined with warm daytime temperatures, this is the Southwest's most productive coniferous forest ecosystem (Moir 1993). The range in mean annual precipitation is typically 600-710 mm, and mean annual temperature is 3-6°C (Moir 1993). Mean annual snowfall is greater than 2.5 m (Beschta 1976 in Moir and Ludwig 1979) and accounts for more of the annual precipitation than summer monsoonal storms.

Lightning is an important component of the climate. A 7,756 km² area of mostly Ponderosa Pine Forest but with some Mixed Conifer Forest in the Jemez Mountains of New Mexico (including BAND) averaged 2.1 cloud-to-ground lightning strikes/ha annually from 1985 to 1994 (Allen 2002).

Soil

Mixed Conifer Forest appears to occur on a variety of soils formed from a variety of parent materials, but the soils are generally deep, permeable, and capable of storing snowmelt. The soil moisture regime, with water available all or most of the growing season, is udic, and the soil temperature regime ranges from the cold extreme of frigid to cryic (Moir 1993).

Soils with Mixed Conifer Forest in Arizona are Alfisols (Typic Eutroboralfs, Typic Glossoboralfs, and Mollic Eutroboralfs) and Entisols (Typic Cryorthents and Typic Ustorthents) (Hendricks 1985). These soils range from shallow to deep, from fine- to moderately coarse-textured, and are mostly well-drained. Soils of the Mixed Conifer Forest in New Mexico are mostly Alfisols with some Mollisols (Maker and Saugherty 1986).

No detailed historical data are available to document changes in soils of the Mixed Conifer Forest, but changes can be inferred from studies of the effects of prescribed burning (see next section).

Stand-Scale Disturbance

Fire - Fire was a key driver of the composition and structure of the Mixed Conifer Forest prior to the beginning of Euro-American influence in the Southwest. However, just as the mosaic landscape structure of this ecosystem was more complex than that of the lower elevation Ponderosa Pine Forest and higher elevation Spruce-Fir Forest, so likely was the fire regime.

As with the Ponderosa Pine Forest, identification of fire as a primary driver of the Mixed Conifer Forest dates back to over a century ago, when Euro-Americans were surveying the resources of the Southwest; however, at that time cultural biases, which led observers to believe that fires were unnatural and that Native Americans were the primary source of ignitions, precluded a clear understanding of the role of fire in this ecosystem (Allen 2002, Swetnam and Baisan 2003). Scientific understanding of fire in Mixed Conifer Forests of the Southwest is recent, dating at least to Dieterich (1983). High-elevation sites remain poorly studied (Swetnam and Baisan 1996).

Although the fire regime prior to Euro-American influence has not been thoroughly studied, there is a growing consensus that it had been a mixed severity fire regime that combined surface and at least patchy crown fires (cf. Jones 1974, Allen 1989, Allen et al. 1995, Touchan et al. 1996). In addition, past fire regimes were likely highly variable among different Mixed Conifer forests in the Southwest, paralleling high diversity in stand composition and structure, as well as in landscape position (Touchan et al. 1996).

A review with data from nine low-elevation Mixed Conifer Forest sites in the Southwest reported ranges for mean fire return intervals for the period 1700-1900 were 3-25 years for fires scarring one or more trees, 9-26 years for fires scarring 10% of scarred trees, and 10-26 years for fires scarring 25% of scarred trees for the period 1700-1900 (compared to 2-17, 4-36, and 4-36 years for 53 ponderosa pine-dominated sites) (Swetnam and Baisan 1996). For low, mid, and high elevation Mixed Conifer Forest sites in GRCA, fire return intervals were 5, 8, and 10 for all fires; 5, 9, and 12 for 10% scarring; and 7, 10, and 19 for 25% scarring (Wolf and Mast 1998). In the Jemez Mountains of New Mexico (including BAND), the range of fire return intervals was 10-14 for all fires and 10% scarring and 10-29 for 25% scarring (Touchan et al. 1996). In each study, unequal sizes of study sites accounts for part of the range in variation.

In general, the fire return intervals for the Mixed Conifer Forest are similar to those of the Ponderosa Pine Forest (however, a critique of the use of fire scars to estimate fire return intervals suggested that return intervals in ponderosa pine forests across the Western United States may be underestimated by an order of magnitude or more; Baker and Ehle 2001). The similarity may reflect researchers focusing on stands of Mixed Conifer Forest that resemble Ponderosa Pine Forest, the lack of fire scarred trees in areas of crown fires, and a synchrony of fires between the two forest ecosystems (Allen et al. 1995, Heinlein 1996). For example, study of low-elevation Mixed Conifer Forest on the San Francisco Peaks near

Flagstaff in northern Arizona found that 37% of fires were synchronous with fires in lower elevation Ponderosa Pine Forest (Heinlein 1996). This suggests that fires frequently moved upslope from Ponderosa Pine Forest to Mixed Conifer Forest. Presumably, such interaction between these forest types would vary depending on landscape features.

Because surface fires dominated the past fire regime of the Ponderosa Pine Forest and crown fires dominated the fire regime of the Spruce-Fir Forest, it appears that the Mixed Conifer Forest must have been a region of transition in fire regimes. However, the transition in fire frequency was not linear (Touchan et al. 1996). The mixed-severity fire regime of the Mixed Conifer Forest consisted of individual fires burning as surface fires in areas conducive to frequent, low-intensity fires (such as drier sites of south and west aspects and ridgetops), but occasionally, if not frequently, crowning in areas of greater, more vertically continuous fuels (such as more mesic sites of north and east aspects and lower slope positions).

The frequency, even the occurrence, of large stand-replacing fires is unclear. Dieterich (1983) reported no evidence of crown fires for the last 300 years in an area of the White Mountains of Arizona and concluded that stand-replacing fires were uncommon in the Mixed Conifer Forest of the Southwest. Lynch and Swetnam (1992) reported stands as old as 500-800 years, indicating that stand-replacing fires were exceedingly uncommon in at least these sites. In contrast, Moir (1993) wrote that stand-replacing fires had been frequent in a Mixed Conifer Forest dominated by white fir and gambel oak and the presence of stands of quaking aspen suggested past crown fires (see also Allen 1989). It appears that areas where surface fires crowned typically were more patchy rather than extensive, but that larger areas of crowning may have occurred with certain climate and fuel conditions.

Fuel for fire is generally always available in the Mixed Conifer Forest, so the limiting factor is moisture (Allen et al. 1995, Swetnam and Baisan 1996, Touchan et al. 1996). Most fires occurred in the summer rather than spring (Dieterich 1983, Heinlein 1996, Wolf and Mast 1998), presumably because fuels were moist from snowmelt in most springs. Also, fires were correlated with reduced winter-spring precipitation (Touchan et al. 1996), and large fires were associated with extreme drought years (Swetnam and Baisan 1996).

Sites where the mixed severity fire regime consisted primarily of surface fires presumably were impacted by fire similarly to the Ponderosa Pine Forest. Here, forest structure was kept within a relatively narrow range of variability, microsites for tree regeneration were produced as reductions in the herbaceous layer lowered competition for germinating seedlings, cohorts of older seedlings and saplings were diminished but the growth of survivors increased, and fuel loads were kept relatively constant. Effects of surface fires on soils can be inferred from studies of prescribed burns in modern Ponderosa Pine Forests: the layer of duff on the soil surface was kept thin and patchy enhancing moisture availability, mineralization was increased thereby increasing nutrient mobilization and nutrients on the soil surface (including nitrogen), and populations of arbuscular mycorrhizae may have increased (for references, see *Ponderosa Pine Forest Ecosystem*).

The high-frequency, low-intensity surface fire component of the mixed-severity fire regime abruptly and dramatically changed in the 19th century (see *Overview*). Numerous studies identified the initial causative factor to be livestock grazing, which reduced the herbaceous layer that formerly provided the continuous fine fuels needed to carry surface fires. Later, active fire exclusion kept most stands free of fire. Without surface fires to consume woody fuels and maintain low densities of trees, fuel loads increased and both horizontal and vertical fuel continuity increased. Therefore, conditions for the crowning component of the mixed-severity fire regime have increased spatially, and fires in the Mixed Conifer Forest now tend to become high-intensity, landscape-scale crown fires.

Wind - Windthrows of single to a few trees occur, at least with ponderosa pine (Pearson 1950), as presumably do blowdowns of small clusters of trees by microbursts. However, there is little in the scientific literature about stand-scale effects of wind on the Mixed Conifer Forest. Windthrows are common on the North Rim of GRCA, possibly as a result of the coarsely textured soils that characterize the region (Fulé et al. 2002a), and wind damage (sometimes augmented by root pathogens) reportedly is

common in Douglas fir, corkbark fir (*Abies lasiocarpa*), and Engelmann spruce (Gottfried 1978).

Pests and Pathogens - The primary insect pest affecting Mixed Conifer Forest is the western spruce budworm (*Choristoneura occidentalis*), a defoliator; indeed, it is considered the most destructive insect pest on western coniferous forests (Fellin and Dewey 1986 in Ryerson et al. 2003). In the Southwest, western spruce budworm feeds primarily on white fir and Douglas fir (Linnane 1986), but also may infest subalpine fir, corkbark fir, Engelmann spruce, and blue spruce (Lynch and Swetnam 1992). Forests most susceptible to infestation are dense, mature, low in vigor, and multi-layered with white fir and Douglas fir as canopy dominants and shade-tolerant species in the understory (Linnane 1986).

Outbreaks can be extensive. For example, 1,076 km² were defoliated in New Mexico in 1987 (USFS 1988 in Moir 1993). Outbreaks are often considered to have become more severe, extensive, and spatially synchronistic with fire exclusion (which resulted in increases in more susceptible species) (e.g., Moir 1993 and research outside the Southwest). However, there is no evidence of increased frequency or severity of outbreaks in northern New Mexico in the 20th century (indeed, the duration of outbreaks became somewhat shorter) (Swetnam 1987). Also, frequency did not change in the 20th century in southwestern Colorado (Ryerson et al. 2003). Moreover, the frequency of outbreaks in older stands in the southern Rocky Mountains is equivalent to that of younger stands (Lynch and Swetnam 1992).

Outbreaks of western spruce budworm had a mean return interval (between initial years of outbreaks) of 34 years in northern New Mexico (Swetnam 1987) and 30-40 years in Colorado and New Mexico (Swetnam and Lynch 1989). Peaks in outbreaks occurred at about 25-50 year intervals, with 83 year intervals for larger outbreaks, in southwestern Colorado (Ryerson et al. 2003). Outbreaks are correlated with an increase in moisture availability after dry periods (Ryerson et al. 2003). Forests that are most susceptible appear to be those already stressed by drought, dwarf mistletoe, high density, root disease, or marginal site conditions (Fellin et al. 1990 in Moir 1993), and forests that have multiple crown layers and greater crown closure (Lynch and Swetnam 1992). Stands can survive multiple outbreaks (Ryerson et al. 2003).

Western spruce budworm feeds primarily on understory trees (Brookes et al. 1987), especially individuals in a weakened condition. Therefore, this defoliating insect acts as a thinning agent (Moir 1993). Overstory mortality occurs with repeated defoliation and with interaction with other pests and pathogens (Linnane 1986). By diminishing seed set and enhancing the mortality of understory seedlings and saplings, western spruce budworm can alter the composition, structure, and dynamics of Mixed Conifer Forests in the Southwest (Lynch and Swetnam 1992, Moir 1993). Forest composition is changed by selective feeding and mortality of Douglas fir and white fir, as well as by opening of gaps that favor regeneration and growth of ponderosa pine, quaking aspen, and southwestern white pine (*Pinus strobiformis*) (Moir 1993). Forest structure is changed by the loss of understory trees, and several defoliations can produce single-storied structure of large Douglas fir and white fir (Moir 1993). Forest dynamics are changed by these factors, and succession can be retarded on drier sites by the loss of shade tolerant trees (Moir 1993).

Other Animals - Elk and deer are the major large ungulates in Mixed Conifer Forests of the Southwest. Animal population dynamics prior to Euro-American influence are unknown, but elk and deer likely affected tree regeneration patterns. For example, regeneration of quaking aspen, a heavily browsed species, would have been reduced during periods of high elk and deer populations. The mixed-severity fire regime likely would have favored elk and deer by increasing sprouts of quaking aspen and by opening stands and enhancing grass cover (Dieterich 1983).

Interactions Among Disturbance Agents - Interactions reported among the above agents of disturbance appear relatively minor. As stated above, fire favors elk and deer. Also, western spruce budworm can weaken trees, making them more susceptible to bark beetle infestation (Lynch and Swetnam 1992). Southwestern dwarf mistletoe can form dense "witches brooms" on trees, and these clusters of branches and foliage can be a fuel ladder for fire to enter the canopy, possibly even resulting in crown fires (Alexander and Hawksworth 1975). Even where fire doesn't crown but remains on the surface, mistletoe can increase tree mortality in fires (Roth 1974, Harrington and Hawksworth 1990).

Unreported but likely interactions include the facilitation of spot crowning of surface fires in areas of small clusters of trees killed by western spruce budworm or bark beetles. In addition, high population densities of elk and deer likely reduced the frequency of surface fires by decreasing the abundance and spatial continuity of grasses and other herbs that fuel surface fires.

Vegetation Dynamics

Given the mixed-severity fire regime in which surface and at least patchy crown fires both occur, succession in the Mixed Conifer Forest can be considered at two scales. In areas of surface fires, succession, if it is to be recognized at all, occurs at the single tree scale (see *Ponderosa Pine Forest Ecosystem*).

In areas of crown fires, succession occurs at the patch or stand scale and likely involves multiple successional pathways, dependent on factors such as trees that survived the fire, the seed- and bud bank that survived the fire, size of the patch, site conditions, and post-fire animal use of the burned area. For example, in New Mexico's Sacramento Mountains, herbs initially dominate sites, but root sprouts of gambel oak and shrubs gradually become dominant, followed by conifers such as ponderosa pine, southwestern white pine, Douglas fir, or white fir, which form a closed canopy 100-200 years following fire (Hanks and Dick-Peddie 1974). In GRCA, conifers are thought to dominate early where seed sources are available, but elsewhere fire is followed by grasses, then quaking aspen, and then conifers (Hurst 1977). In the Jemez Mountains of New Mexico (including BAND), today's stands of quaking aspen represent areas of patchy stand-opening fires dating to the late 19th century (Touchan et al. 1996). With the increase in fuels following fire exclusion, crown fires and stand-scale succession are expected to become more common and more widespread.

Composition and Structure

The Mixed Conifer Forest has highly variable stand composition and structure. This diversity of stands has led to the development of many classifications (e.g., Moir and Ludwig 1979, White and Vankat 1983, Alexander et al. 1984, DeVelice et al. 1986). Most classifications provide detail that is excessive for the purpose of this report; therefore, this section focuses on broad gradients to provide insight into composition and structure.

Trees

Before Euro-American Influence - The Mixed Conifer Forest apparently consisted of a complex mosaic of patches that differed not only in species composition but also in stand structure (Moir 1993, White and Vankat 1993). Generally, however, the forest was more open than it is today (Moir 1993, Heinlein 1996), and stands of quaking aspen were more abundant (Dieterich 1983, Bartos 2001). The high frequency of fire favored regeneration of ponderosa pine, quaking aspen, and Douglas fir (Moir 1993, White and Vankat 1993), while restricting the development of canopy-sized white fir to cooler, moister sites where fires were less frequent (White and Vankat 1993, Heinlein 1996) and/or less regular in their periodicity. The conifer-quaking aspen mosaic was likely more clearly defined (Dieterich 1983) with the mixed-severity fire regime.

More specifically, stands in drier sites such as south and west aspects and ridgetops were nearly solely dominated by ponderosa pine (Dieterich 1983). Present day observations of such sites indicate that these stands likely had an open structure and were very similar, if not identical, to stands of Ponderosa Pine Forest. Therefore, although the exact nature of stands would have differed site to site, it is likely that many stands were open and park-like, dominated by an overstory of large ponderosa pines and an understory of patchy reproduction of ponderosa pine and, especially in wetter periods, other conifers such as Douglas fir -- all above a dense herbaceous layer dominated by grasses. In other words, these stands were more woodland than forest. Presumably, these drier sites had the highest fire frequencies of any Mixed Conifer Forest stands. Frequent, low-intensity surface fires would have maintained the open physiognomy by thinning patches of reproduction and leaving a multi-aged forest (for more detail and references, see *Ponderosa Pine Forest Ecosystem*).

With increasing moisture availability along gradients of slope aspect, slope position, and elevation, tree

composition shifted. Stands likely had less ponderosa pine and more Douglas fir, white fir, blue spruce, and others. The structure of today's stands in the middle portion of the topographic-moisture gradient suggests that these Mixed Conifer Forest stands were also open (although perhaps not as open as the ponderosa pine-dominated drier sites). For example, Dieterich (1983) reported finding scattered old trees of nearly all species. The presence of these scarred trees supports the hypothesis that surface fires were frequent in these stands.

Forest reconstruction of two low- to mid-elevation stands of Mixed Conifer Forest on the San Francisco Peaks near Flagstaff, Arizona indicated a former mean density of 52 trees/ha (for trees >2.5 cm dbh) and total basal area ranging from 9.1 to 12.4 m²/ha (Heinlein 1996). The stands were 50-83% ponderosa pine, with other conifers clustered and averaging 8.3-14.3 trees/ha and 3.6-3.8 m²/ha. Leiberg et al. (1904) similarly described an area of Mixed Conifer Forest in the same region. The fire regime in these stands likely had greater frequency of patchy crowning and thereby created more areas where quaking aspen was abundant. Forest reconstruction for trees >2.5 cm dbh in a high elevation area of GRCA indicated a density of 246 trees/ha (range of 90-374) and a basal area of 29 m²/ha in 1879 (Fulé et al. 2002a).

Stands of Mixed Conifer Forest further toward the mesic end of the topographic-moisture gradient likely had still less ponderosa pine and more white fir, Douglas fir, blue spruce, and species of the Spruce-Fir Forest, i.e., Engelmann spruce and subalpine fir. The coolest, most mesic sites likely were dominated by blue spruce, especially in low slope positions along drainages and along margins of meadows (Moir 1993, White and Vankat 1993). Stands near streams and in other highly mesic areas were likely denser than most stands, presumably as a result of lower fire frequencies. These areas would have experienced crown fires.

Superimposed on the mosaic related to the topographic-moisture gradient is a mosaic based on disturbance and succession (Swetnam and Lynch 1989, Swetnam 1990, Moir 1993). A primary early successional tree, especially in mesic sites, was quaking aspen. This species formed dense patchy stands in areas of crowning, either by enhanced root sprouting following fire or by seed dispersal from other stands.

In addition to stands of Mixed Conifer Forest occurring within the usual elevational range, isolated stands of scattered individuals of Douglas fir are present in several units of SCPN, including GLCA (Tuhy and MacMahon 1988, Spence 1995). These stands occur in cool, moist sites with deep, well-drained soils at the bases of north-facing cliffs or alcoves, often where there are springs. They occur at approximately 1,700-2,000 m, surrounded by Pinyon-Juniper Woodland. These low-elevation disjuncts may be relicts of cooler, moister periods of the Late-Glacial or early Holocene when Douglas fir typically occurred at such elevations, or they may be products of long-distance dispersal (Spence 1995).

With Euro-American Influence - The reduced fire frequencies accompanying livestock grazing and, later, fire exclusion activities, dramatically changed the structure and composition of stands of Mixed Conifer Forest (Dieterich 1983, Allen 1989, Moir 1993, White and Vankat 1993, Heinlein 1996, Dahms and Geils 1997, Fulé et al. 2002a), as well as landscapes of Mixed Conifer Forest (White and Vankat 1993, Ryerson et al. 2003). Stand-level changes included shifts in forest structure (densities, distribution of diameter classes, structural diversity, and tree vigor) and in species composition. Landscape-level changes include greater homogeneity and larger patch size ([Figure 6](#)).

Most quantitative research has focused on the change in forest densities -- it is the most visually obvious change and, perhaps, the one most amenable to attempts to quantify. At two low- to mid-elevation sites on the San Francisco Peaks, mean density (for trees >2.5 cm dbh) was projected to have increased 1836% (52 to 1007 trees/ha) and 3002% (from 52 to 1007-1613 trees/ha), and total basal area increased 311% (from 9 to 37 m²/ha) and 333% (from 12 to 52 m²/ha) (Heinlein 1996). In addition, the relative abundance of ponderosa pine declined about 68% (from 50 to 16% and from 83 to 27%). For a high-elevation Mixed Conifer area in GRCA, mean density (for trees >2.5 cm dbh) increased 283% (from 246 to 941 trees/ha; ranges: 90-374 to 309-2,418 trees/ha) and mean basal area increased 41% (from 29 to 41 m²/ha; ranges: 15-54 to 19-62 m²/ha) (Fulé et al. 2002a). Canopy cover at this site averaged 63%

The distribution of diameter classes has shifted toward greater abundance of smaller trees (Dahms and Geils 1997). Many of the small trees are white fir and other shade-tolerant, fire-sensitive species, which formerly had been thinned by surface fires (Merkle 1962, White and Vankat 1993, Dahms and Geils 1997, Bastian 2001). The increased extent and density of small trees increased stand and landscape homogeneity (White and Vankat 1993, Ryerson 2003), as well as increased horizontal and vertical fuel continuity (White and Vankat 1993, Heinlein 1996). Landscape homogeneity also increased as stands of quaking aspen became less common with fire exclusion as conifers overtopped and replaced quaking aspen in succession (e.g., Dahms and Geils 1997, Bartos 2001). The increase in homogeneity and fuel continuity has increased the probability of crown fires (Swetnam and Lynch 1992, White and Vankat 1993, Heinlein 1996, Dahms and Geils 1997). Crown fires may serve to perpetuate the current homogeneity of the Mixed Conifer Forest (White and Vankat 1993).

Tree vigor has likely declined as a result of increased density of small trees (see *Ponderosa Pine Forest Ecosystem* for details and references), although the greater moisture availability of mesic sites in the Mixed Conifer Forest may have ameliorated the effect reported for the Ponderosa Pine Forest. Mortality from 1935 to recent studies for conifers ≥ 60 cm dbh was 85% in low-elevation (transitional) stands of Mixed Conifer Forest in GRCA (Crocker-Bedford et al. 2003)

Circa 1880 - more heterogeneous with smaller patches

The diagram shows a cross-section of a landscape with a valley bottom and a ridgetop. The forest stands are more heterogeneous with smaller patches. The stands are labeled as follows:

- Valley Bottom: Dense BS Stand
- South-facing Aspect: Open PP & DF Stand
- Ridgetop: Open Canopy PP Stand
- North-facing Aspect: Moderately Dense Mixed Species Stand
- Left Slope: Moderately Dense Mixed Species Stand

Today - more homogeneous with larger patches

The diagram shows a cross-section of a landscape with a valley bottom and a ridgetop. The forest stands are more homogeneous with larger patches. The stands are labeled as follows:

- Valley Bottom: Dense BS Stand
- South-facing Aspect: Dense Mixed Species Stand
- Ridgetop: PP Canopy & WF Understory Stand
- North-facing Aspect: Dense Mixed Species Stand
- Left Slope: Dense Mixed Species Stand

Shrubs and Herbs Little or nothing is known about the shrub and herb understory of the Mixed Conifer Forest before or near the beginning of Euro-American influence. It is likely, however, that at least the drier stands dominated by ponderosa pine were similar to stands of the Ponderosa Pine Forest in which there was a sparse shrub layer and a dense herb layer dominated by grasses (see *Ponderosa Pine Forest Ecosystem*). The understory in mesic areas was likely even better developed in open stands, but less developed in areas of denser canopy.

With only rudimentary knowledge of former conditions, most descriptions of changes in shrubs and herbs refer to generalized qualitative changes related to increases in forest density and duff on the soil surface (cf. Pase and Brown 1994a, Dahms and Geils 1997). Today, some areas, particularly lower elevation openings, have a shrubby understory, but cover varies greatly (Merkle 1962, Moir 1993). The herb layer is greatly reduced in areas where white fir has become abundant with fire exclusion (Merkle 1962). Total plant cover on a site in GRCA was about 18% (Springer et al. 2000).

More detailed information, including species lists, is available (cf. Merkle 1962, Moir 1993, Pase and Brown 1994a, Springer et al. 2000).

Animals

The New Mexico Department of Fish and Game maintains a searchable website (<http://nrmnhp.unm.edu/bisonm/bisonquery.php>) which lists animal taxa for Mixed Conifer Forest in New Mexico and Arizona. Currently, the site lists 31 molluscs, 3 amphibians, 8 reptiles, 106 birds, and 139 mammals, second most in each category behind the Ponderosa Pine Forest (except third for reptiles behind the Montane Shrubland and Ponderosa Pine Forest). Of course many of the taxa listed have ranges that extend outside the Mixed Conifer Forest.

Little information is available on the history of most species (Dahms and Geils 1997), but the New Mexico Department of Fish and Game considers some of the taxa listed on their website as extirpated and extinct. All six extirpated species and the one extinct species of the Mixed Conifer Forest are mammals.

Additional listings are available for stands dominated by quaking aspen: no molluscs, 4 amphibians, 3 reptiles, 83 birds, and 121 mammals.

Anthropogenic Stressors

The major anthropogenic stressors affecting or potentially affecting the Mixed Conifer Forest of SCPN are fire exclusion, exotic species, and air pollution. Visitors to SCPN units have relatively little direct impact, because high use areas are concentrated in lower elevations.

The impact of fire exclusion on soils, vegetation dynamics, and ecosystem structure and composition is covered above.

What few data are available on exotic species suggest that currently they are not a major stressor. In an area of Mixed Conifer Forest in GRCA, exotics accounted for less than 2% of plant ground cover (Springer et al. 2000). Smooth brome was the only species listed.

Little is known about air pollution effects on the Mixed Conifer Forest of the Southwest. Ozone levels at the south rim of GRCA, measured by the ozone SUM 06 statistic, reached 27 ppm-hrs in 1996, 28 ppm-hrs in 1998, and 31 ppm-hrs in 1999 (Bowman 2003). Foliar injury on ponderosa pines was 15-50% at 25-30 ppm-hrs in Lassen Volcanic, Sequoia/Kings Canyon, and Yosemite National Parks in California (NPS 2002). This suggests that ozone may be impacting at least the ponderosa pines of the Mixed Conifer Forest in GRCA and possibly other SCPN units

Figure 7. Ecosystem characterization model of Mixed Conifer Forest. Symbols are as follows: rectangles = biotic components, ovals = interactive controls, solid rounded rectangles = state factors, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships. Numbers next to relationships are keyed to [Table 3](#).

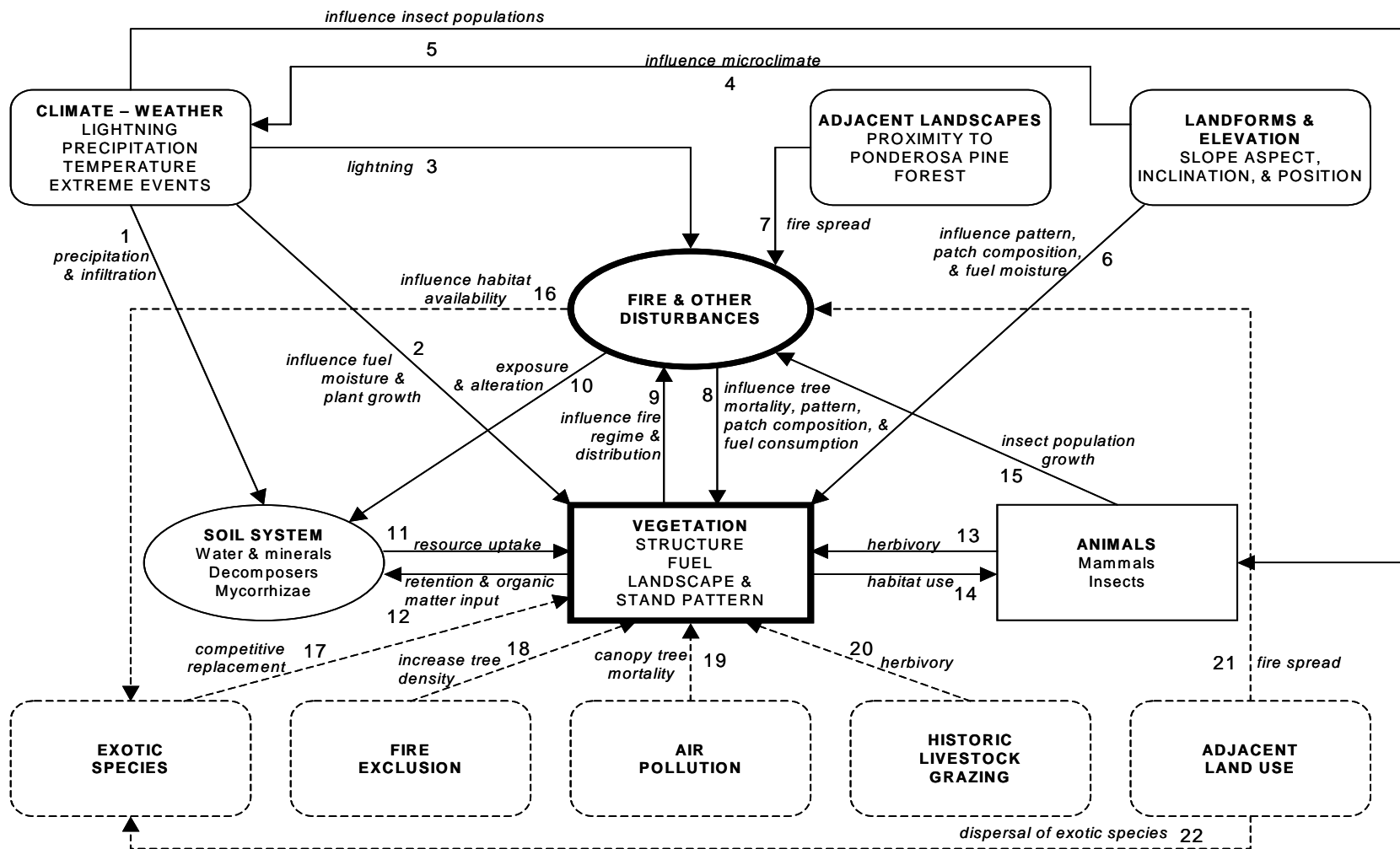


Table 3. Explanation of relationships shown in ecosystem characterization model of Mixed Conifer Forest. Numbers for relationships are keyed to [Figure 7](#).

Relationships	Circa 1880	Today
1	Precipitation & infiltration add to soil moisture. Snowmelt of winter snowpack is critical in recharging soil moisture (see text for details).	Same, but in addition, infiltration of summer monsoonal rain and, to a lesser degree, winter snowmelt is reduced by thick layer of duff.
2	Precipitation and evaporation determine moisture level of fuel, and climate is major factor determining plant growth.	Same.
3	Lightning ignites fires.	Same.
4	Landforms, especially slope aspect, result in microclimate variation. Elevation affects precipitation and evapotranspiration.	Same, except that in some areas denser tree cover reduces microclimate variation on the soil surface
5	Precipitation and evaporation effect populations of western spruce budworm (see text for details).	Same
6	Variation in landforms contributes to heterogeneous vegetation pattern in which tree densities and composition differ among and within stands. Elevational differences also affect species composition.	Same; however, impact of landform variation on microclimate is reduced in areas with denser tree cover.
7	Fires spread into ecosystem from lower elevation Ponderosa Pine Forest.	Same, but much less frequently because of fire exclusion
8	In dry and moderate sites, surface fires thin patches of tree regeneration, heterogeneous surface fire pattern contributes to a heterogeneous vegetation pattern, and fuels are consumed by frequent surface fires, precluding buildup of fuels between fires. In moist sites, crown fires kill trees in all size classes (see text for details), western spruce budworm infestations kill understory white fir and Douglas fir (thereby producing fine and coarse fuels), crown fire pattern reinforces a homogeneous vegetation pattern, and fuels build up between infrequent crown fires and are mostly consumed in fires.	Crown fires kill trees in all size classes, and western spruce budworm infestations kill understory white fir and Douglas fir (thereby producing fine and coarse fuels). In dry and moderate sites with a crown fire regime, more homogeneous fire pattern reinforces a more homogeneous vegetation pattern and fuels build up between infrequent crown fires and are mostly consumed in fires.
9	In dry and moderate sites, light fuel load, horizontally continuous, annually regenerated fine fuel on forest floor; and vertically discontinuous fuel result in fire regime of frequent, low intensity surface fires. In addition, heterogeneous vegetation pattern combines with surface fire regime to produce a heterogeneous fire pattern. In moist sites, heavier fuel load and vertically continuous fuel result in fire regime of infrequent, high intensity crown fires (see text for details). In addition, homogeneous vegetation pattern and high fuels combine with crown fire regime to produce a homogeneous fire pattern.	In dry and moderate sites, heavier fuel loads and vertically continuous fuel result in fire regime of infrequent, high intensity crown fires (see text for details). In addition, a more homogeneous vegetation pattern and high fuels combine with a crown fire regime to produce a homogeneous fire pattern
10	In dry and moderate sites, surface fires partially and patchily expose soil surface. In moist sites, crown fires expose soil surface and alter soil properties.	In dry and moderate sites with crown fire regime, fires expose soil surface and alter soil properties.
11	Water and minerals in soil are absorbed by plants.	Same, but water and minerals may be less available.
12	Plants stabilize soil and produce coarse woody debris and litter.	Same
13	Herbivores graze vegetation. Unusually high deer populations can reduce the herb layer.	Same.
14	Vegetation serves as habitat for animals.	Same, but habitat in at least dry and moderate sites is different.
15	Population growth of western spruce budworm leads to insect infestations.	Same
16	Not applicable.	Disturbance inside SCPN units creates habitat for exotic species.
17	Not applicable.	Exotic species successfully compete with native species. Some exotics may have the potential to alter ecosystem processes.

Relationships	Circa 1880	Today
18	Not applicable.	Fire exclusion by NPS results in increased tree density.
19	Not applicable.	Ozone and other air pollutants may increase the mortality of canopy trees of ponderosa pine (see text for details).
20	Not applicable.	Livestock grazing removed fine fuels (by consuming herbaceous plants) and likely changed species composition.
21	Not applicable.	Human-caused fires originating outside SCPN units may spread into units.
22	Not applicable.	Disturbances in lands adjacent to SCPN units provide habitat for establishment of exotic species, which are then more likely to be dispersed into the units.

Figure 8a. Ecosystem dynamics model of Mixed Conifer Forest on dry sites such as ridgetops and south aspects. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model ([Figure 7](#)) by showing the various communities (within different states) and processes that form them. Numbers next to relationships and letters next to transitions are keyed to [Table 4a](#). Compare to [Figures 8b](#) and [c](#) for full coverage of the Mixed Conifer Forest.

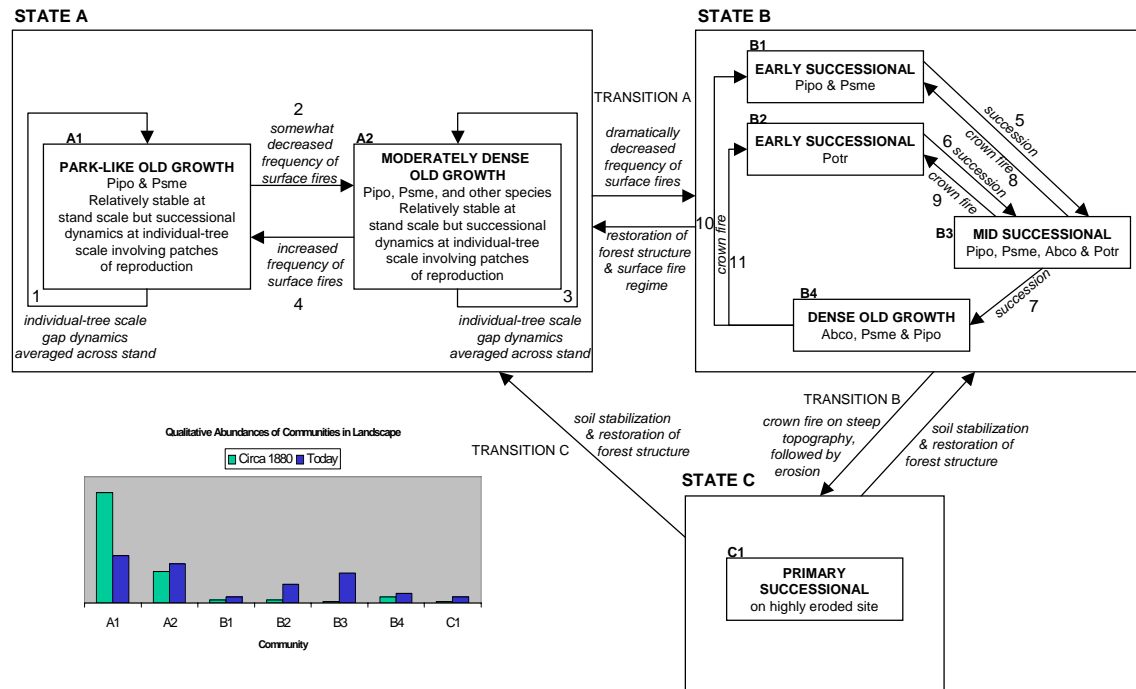


Table 4a. Explanation of relationships and transitions shown in ecosystem dynamic model of Mixed Conifer Forest on dry sites such as ridgetops and south aspects. Numbers for relationships and letters for transitions are keyed to [Figure 8a](#).

Relationships and Transitions	Circa 1880	Today
1	Treefalls of single to a few trees, followed by surface fire, result in regeneration of trees that, after thinning by additional surface fires, replace the original canopy tree(s) (see text for details).	Same, at least in sites with low tree density.
2	A relatively small decrease in fire frequency induced by climate leads to an increase in stand density.	Same, at least in sites with low tree density.
3	Treefalls of single to a few trees, followed by surface fire, result in regeneration of trees that, after thinning by additional surface fires, replace the original canopy tree(s) (see text for details).	Same, at least in sites with moderate tree density.
4	A relatively small increase in fire frequency induced by climate leads to a decrease in stand density.	Same, at least in sites with moderate tree density.
5	In sites without quaking aspen, succession leads from early to mid successional stands. Uncommon.	Same, but more common.
6	In sites with quaking aspen, succession leads from early to mid successional stands. Uncommon.	Same, but more common.
7	Succession leads from mid successional to old-growth stands. Uncommon.	Same, but more common.
8	Crown fire replaces mid successional stand, in which quaking aspen was absent, with early successional stand. Uncommon.	Same, but more common.
9	Crown fire replaces mid successional stand, in which quaking aspen was present, with early successional stand. Uncommon.	Same, but more common.

Relationships and Transitions	Circa 1880	Today
10	Crown fire replaces old growth in which quaking aspen was absent, leading to the establishment of an early successional stand of ponderosa pine and Douglas fir. Uncommon.	Same, but more common.
11	Crown fire replaces old growth in which quaking aspen was present, leading to the establishment of an early successional stand dominated by quaking aspen. Uncommon.	Same, but more common.
A	Uncommon.	Fire exclusion takes stands from State A to State B (see text for details). Reversion to State A requires restoration of forest structure and surface fire regime.
B	Uncommon.	Crown fire on steep topography may be followed by severe soil erosion, taking stands from State B to State C. Reversion to State B requires soil stabilization and restoration of forest structure.
C	Uncommon.	Transition to State A requires soil stabilization and restoration of forest structure.

Figure 8b. Ecosystem dynamics model of Mixed Conifer Forest on intermediate sites such as north aspects. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model ([Figure 7](#)) by showing the various communities (within different states) and processes that form them. Numbers next to relationships and letters next to transitions are keyed to [Table 4b](#). Compare to [Figures 8a](#) and [c](#) for full coverage of the Mixed Conifer Forest.

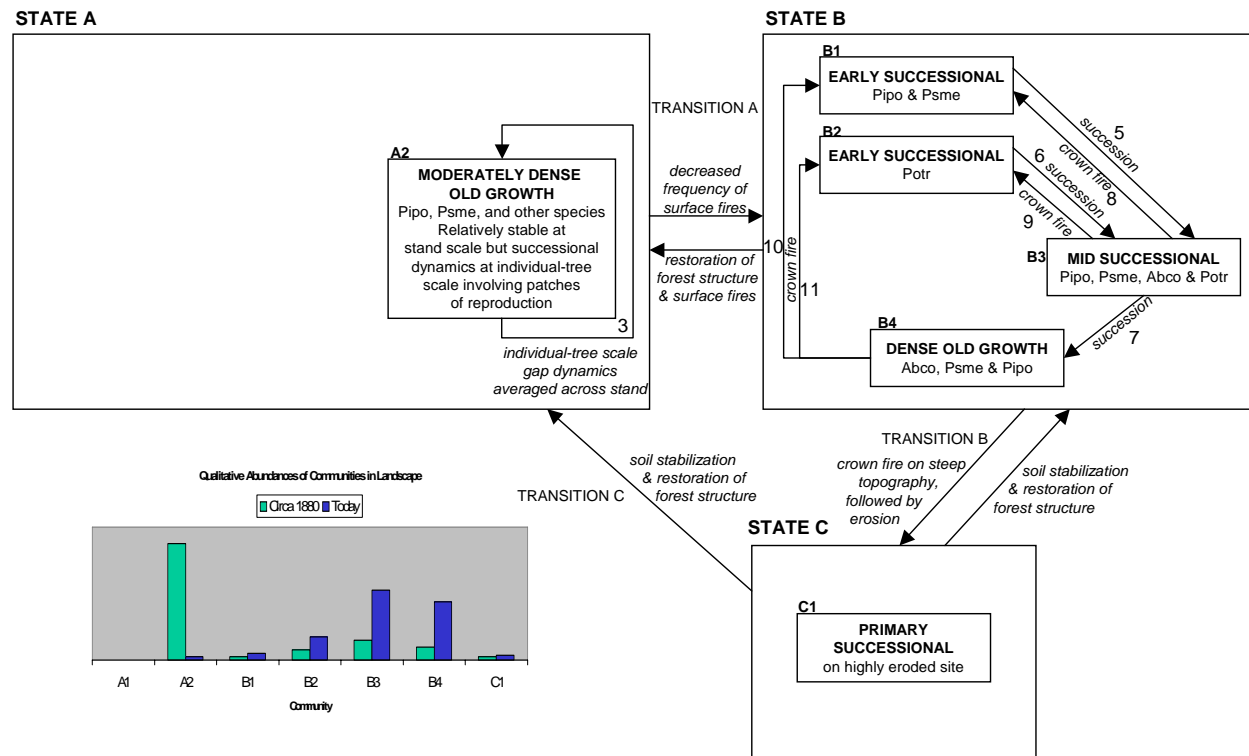


Table 4b. Explanation of relationships and transitions shown in ecosystem dynamic model of Mixed Conifer Forest on intermediate sites such as north aspects. Numbers for relationships and letters for transitions are keyed to [Figure 8b](#).

Relationships and Transitions	Circa 1880	Today
3	Treefalls of single to a few trees, followed by surface fire, result in regeneration of trees that, after thinning by additional surface fires, replace the original canopy tree(s) (see text for details).	Same, at least in sites with moderate tree density.
5	In sites without quaking aspen, succession leads from early to mid successional stands.	Same, but more common.
6	In sites with quaking aspen, succession leads from early to mid successional stands.	Same, but more common.
7	Succession leads from mid successional to old-growth stands.	Same, but more common.
8	Crown fire replaces mid successional stand, in which quaking aspen was absent, with early successional stand. Uncommon.	Same, but more common.
9	Crown fire replaces mid successional stand, in which quaking aspen was present, with early successional stand. Uncommon.	Same, but more common.
10	Crown fire replaces old growth in which quaking aspen was absent, leading to the establishment of an early successional stand of ponderosa pine and Douglas fir. Uncommon.	Same, but more common.
11	Crown fire replaces old growth in which quaking aspen was present, leading to the establishment of an early successional stand dominated by quaking aspen. Uncommon.	Same, but more common.

Relationships and Transitions	Circa 1880	Today
A	Uncommon.	Fire exclusion takes stands from State A to State B (see text for details). Reversion to State A requires restoration of forest structure and surface fire regime.
B	Uncommon.	Crown fire on steep topography may be followed by severe soil erosion, taking stands from State B to State C. Reversion to State B requires soil stabilization and restoration of forest structure.
C	Uncommon.	Transition to State A requires soil stabilization and restoration of forest structure.

Figure 8c. Ecosystem dynamics model of Mixed Conifer Forest on moist sites such as drainages. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model (Figure 7) by showing the various communities (within different states) and processes that form them. Numbers next to relationships are keyed to Table 4c. Compare to Figures 8a and b for full coverage of the Mixed Conifer Forest.

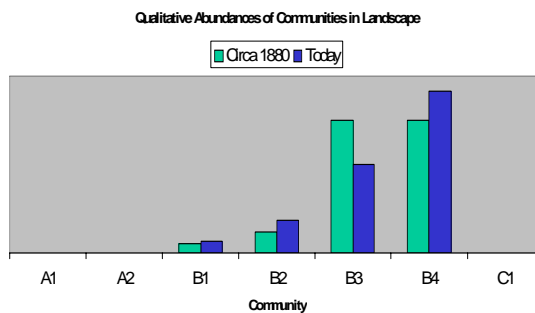
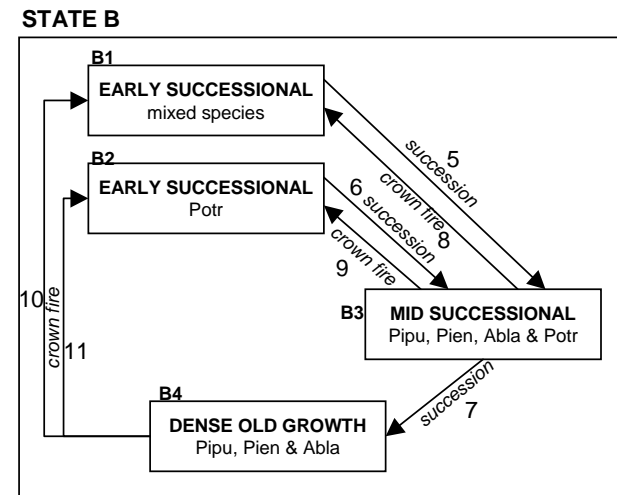
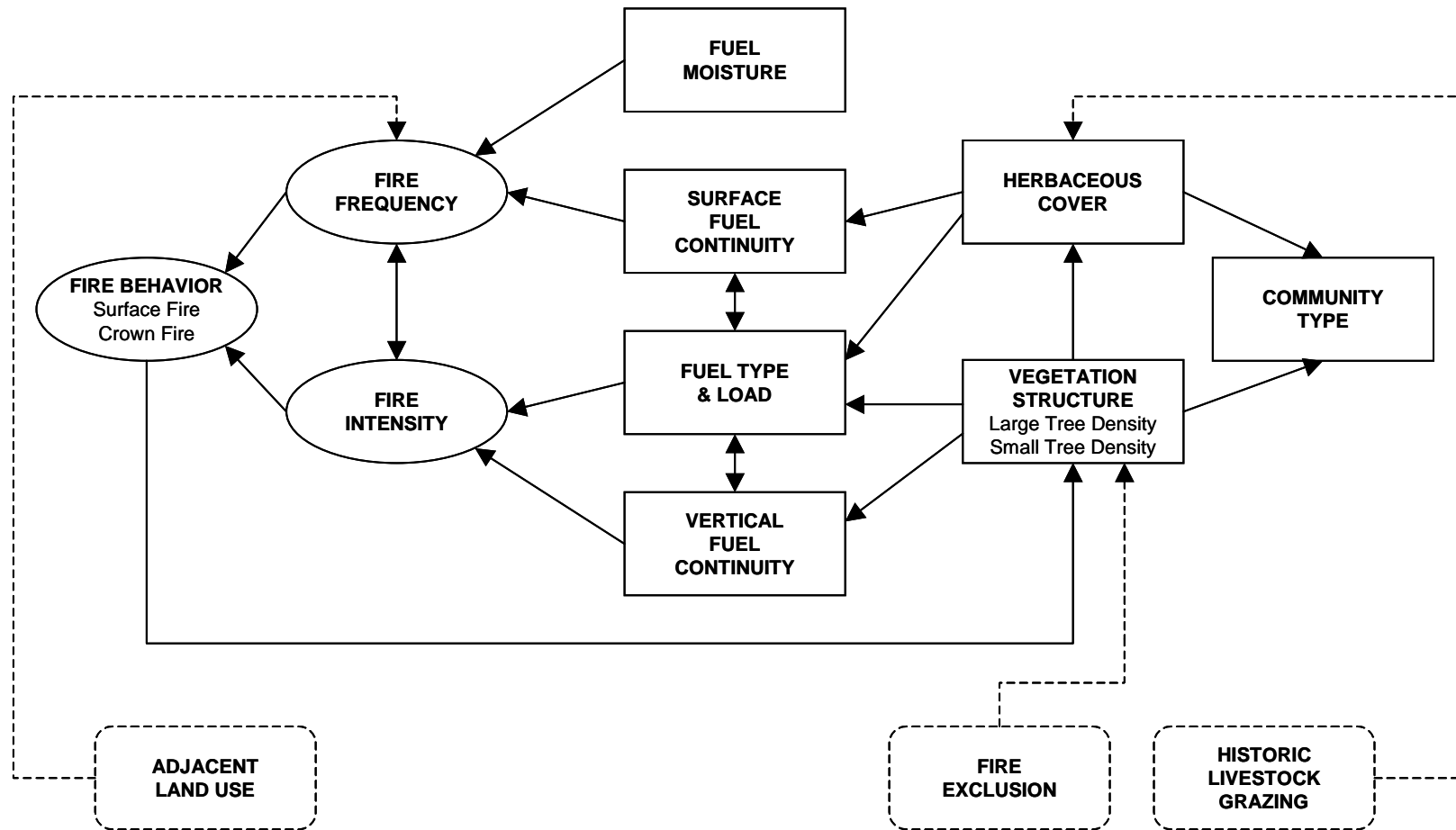


Table 4c. Explanation of relationships shown in ecosystem dynamic model of Mixed Conifer Forest on moist sites such as drainages.
Numbers for relationships are keyed to [Figure 8c](#).

Relationships	Circa 1880	Today
5	In sites without quaking aspen, succession leads from early to mid successional stands.	Same, but more common.
6	In sites with quaking aspen, succession leads from early to mid successional stands.	Same, but more common.
7	Succession leads from mid successional to old-growth stands.	Same, but more common.
8	Crown fire replaces mid successional stand, in which quaking aspen was absent, with early successional stand. Uncommon.	Same, but more common.
9	Crown fire replaces mid successional stand, in which quaking aspen was present, with early successional stand. Uncommon.	Same, but more common.
10	Crown fire replaces old growth in which quaking aspen was absent, leading to the establishment of an early successional stand of ponderosa pine and Douglas fir. Uncommon.	Same, but more common.
11	Crown fire replaces old growth in which quaking aspen was present, leading to the establishment of an early successional stand dominated by quaking aspen. Uncommon.	Same, but more common.

Figure 9. Mechanistic model of Mixed Conifer Forest. This model provides more detail on the mechanisms involved in the vegetation - fuel - fire interaction of the ecosystem dynamics models ([Figures 8a, b, c](#)). Symbols are as follows: rectangles = biotic components, ovals = interactive controls, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships.



Spruce-Fir Forest Ecosystem

Forest ecosystems dominated by Engelmann spruce and subalpine fir are uncommon in the Southwest, covering less than 0.5% (478 km²) of Arizona and less than 2% (1,501 km²) of New Mexico (Moir and Ludwig 1979; Alexander 1987). The Spruce-Fir Forest accounts for less than 3% of the land area within the units of SCPN and is present in only two units: GRCA and BAND.

Although little research has been done on Spruce-Fir Forest in the southern Colorado Plateau, more has been done in nearby regions, including isolated mountains south of the Plateau and, especially, in the Rocky Mountains of Colorado where Spruce-Fir Forest is much more widespread. Research findings from these regions provide much of the basis for this review.

Ecosystem Constraints and Drivers

Topography

Spruce-Fir Forest occurs in the highest forested elevations of the Southwest, i.e., the subalpine zone, from about 2,450 m to 3,500-3,800 m (Pase and Brown 1994b). The lower elevational limit is indistinct because of a sometimes patchy intergradation with Mixed Conifer Forest. The upper elevational limit (where present) is near or at treeline (some locations have a specialized treeline community).

Within GRCA, Spruce-Fir Forest occupies the highest elevations of the Kaibab Plateau, generally 2,650-2,800 m, but lower on steep mesic slopes and in narrow valleys (Merkle 1954, White and Vankat 1993). In more detail, Spruce-Fir Forest occurs across a topographic-moisture gradient above 2,700 m, but is limited to the most moist third of the gradient down to 2,500 m (the lowest elevation sampled) (White and Vankat 1993). Therefore, elevations between 2,500 and 2,700 m have a mosaic of forests, with Spruce-Fir Forest on moister sites such as north and east aspects and valley bottoms and Mixed Conifer Forest on drier slope aspects and positions. Investigation of a low elevation Spruce-Fir dominated landscape in GRCA revealed small differences in mean elevation among stands of Spruce-Fir Forest (2,860 m), Mixed Conifer Forest (2,666 m), and Ponderosa Pine Forest (2,629 m), illustrating that the mosaic was largely based on topographic factors other than elevation (Fulé et al. 2002b). For example, systematic grid sampling suggested that Ponderosa Pine Forest was restricted to steep south- and west-facing slopes.

Climate

Climate data from high-elevation sites are spottily available at best and are entirely lacking from SCPN. In general, the climate of Spruce-Fir Forest of the Southwest is characterized by cool temperatures, with a mean annual temperature of 2°C, ranging from -7 to -9°C in January to 10 to 16°C in July (Alexander 1987). The cool temperatures result in a short growing season of less than 75 days (Alexander 1987, Pase and Brown 1994b). Annual precipitation is 610 to >1,000 mm (Alexander 1987, Pase and Brown 1994b) and follows the typical bimodal pattern of the Southwest. Snowfall averages >5 m (Alexander 1987) (3.28 m in GRCA, Fulé et al. 2002b) and accumulates in the winter. Extreme droughts occur occasionally (Alexander 1987). The patchy distribution of Spruce-Fir Forest at lower elevations, where it intergrades with Mixed Conifer Forest, appears at least in part related to microclimatic variation accompanying differences in slope aspect and position (Merkle 1954, Dye and Moir 1977, White and Vankat 1993).

Lightning is an important component of the climate. GRCA records for 1967-1996 indicate 38 lightning fires (1.3/year) within an approximately 4,400 ha area of mostly Spruce-Fir Forest (Fulé et al. 2002b).

Soil

Data on soils are also spotty. Subalpine soils in the Rocky Mountains vary according to the rock parent material, but are generally relatively deep (especially at lower elevations; Moir 1993), permeable, and capable of storing snowmelt (Leaf 1975). Southwestern subalpine soils tend to be covered with thick duff (Pase and Brown 1994b). In addition, the soil moisture regime tends to be udic, and the soil temperature regime is cryic (DeVelice et al. 1986, Moir 1993).

Soils of the Spruce-Fir Forest in Arizona are Typic Argiborolls, Argic Pachic Cryoborolls, Typic

Glossoboralfs, and Lithic Cryoborolls, with the latter two present in GRCA (Hendricks 1985). These soils range from shallow to deep, from fine- to medium-textured, and from moderately to well-drained.

Subalpine soils in southern New Mexico tend to have formed from intrusive parent materials and were characterized as coarse-loamy, Pachic Cryoborolls with dark A horizons (Dye and Moir 1977). Analysis of the surface soil (0-2 cm depth) indicated that old-growth stands had higher organic matter, pH, nitrogen, phosphorus, calcium, manganese, sodium, and potassium than younger strands.

Stand-Scale Disturbance

Spruce-Fir Forest in general is characterized by infrequent, stand-scale disturbance. Agents of disturbance are fire, wind, and pests and pathogens.

Fire - Little research has been done on fire regimes of Spruce-Fir Forest of the Southwest, at least in comparison to Ponderosa Pine Forest (Moir 1993, Swetnam and Baisan 1996, Allen 2002). In part, this reflects the paucity of stands of Spruce-Fir Forest (Fulé et al. 2002b). In addition, with both Engelmann spruce and subalpine fir thin-barked and unlikely to survive fires, trees with fire scars are rare, limiting research on fire regimes (Veblen et al. 1994).

Nevertheless, there is ample evidence that fire is an important natural driver of Spruce-Fir Forest, with evidence from the Southwest (Leiberg et al. 1904, Grissino-Mayer et al. 1995, Fulé et al. 2002b) and nearby regions (Baker and Veblen 1990, Veblen et al. 1991a, 1994, Peet 2000). More specific to SCPN, charred logs and stumps have been reported throughout the Spruce-Fir forest in GRCA (Merkle 1954). Most fires burned in summer rather than spring (Fulé et al. 2002b).

Fires in the subalpine zone have been characterized, at least for Colorado, as of three kinds, surface, mixed-severity (or patch), and crown fires (Baker and Veblen 1990). Surface fires were likely uncommon, as evidence is only anecdotal.

Mixed-severity fires burned on the order of decades and were more common in the past (Jones 1974, Dieterich 1983, Moir 1993). This kind of fire regime was implied for an area of GRCA in a report of fire return intervals varying from 70 to 250 years (White and Vankat 1993). Elsewhere in GRCA, an area largely of Spruce-Fir Forest had a mean fire interval from 1700 to 1879 of only 8.8 years for fires scarring 10% of scarred trees, and only five large fires (scarring at least 25% of scarred trees) occurred (they were correlated with dry years that generally followed several wet years) (Fulé et al. 2002b). Mixed-severity fires possibly never reached a stable distribution in the past (Fulé et al. 2002b), and may be less common today with higher fuel levels resulting from fire exclusion (Moir 1993).

Crown fires may be expected where the cool, damp environment reduces the probability of fires and fuels build up between fires. When crown fires do occur, in some areas they are augmented by steep topographic relief. A fire regime of infrequent, high intensity crown fires has been described by numerous authors for GRCA (e.g., Merkle 1954, White and Vankat 1993, Fulé et al. 2002b). Elsewhere, such fires are thought to have burned on the order of centuries (Swetnam 1990). Maximum tree ages may indicate infrequent fire (but do not necessarily date past fire, in part because succession may begin with short-lived quaking aspen) (Fulé et al. 2002b). Tree ages of 275 years have been reported for Spruce-Fir Forest in southern New Mexico (Dye and Moir 1977) and over 300 years in southeastern Arizona (Grissino-Mayer et al. 1995). Distributions of even-aged, presumably post-fire stands in Colorado suggested a fire interval of 300 years (Clagg 1975 in Veblen et al. 1994). Peet (1981) suggested a fire interval of 200-400 years. In an area of approximately 600 ha of mostly Spruce-Fir Forest in northwestern Colorado, mean return intervals for fire were 202 years, while fire turnover time was 521 years (Veblen et al. 1994).

Perhaps regardless of type of fire, the occurrence of fire in the Spruce-Fir Forest is likely dependent more on the moisture level than the amount of fuel.

There is a widespread belief that the fire regime of the Spruce-Fir Forest has changed little since the beginning of Euro-American influence (e.g., White and Vankat 1993). This hypothesis is based on the

argument that the period of fire exclusion (perhaps 50-75 years, depending on location) has not exceeded the normal fire intervals occurring before Euro-American influence. However, where fire exclusion has altered stands by reducing surface and mixed-severity fires, landscape mosaics have become more homogeneous and are susceptible to large-scale, homogeneous crown fires (White and Vankat 1993, Fulé et al. 2002b).

Wind - Wind has been under-recognized as a possible important disturbance factor in Spruce-Fir Forest of the Southwest (although see White and Vankat 1993). For example, in a review of forest ecosystem health in the Southwest, Dahms and Geils (1997) ignored wind in stating that "The major disturbances in the spruce-fir forests of the Southwest are fire and bark beetles".

In contrast, wind has been identified as an important disturbance agent in Spruce-Fir Forests in the Rocky Mountains of Colorado (Alexander and Buell 1955, Alexander 1987, Veblen et al. 1989, 1991a, 1991b, 2001). For example, blowdowns (involving 3 or more canopy trees) covered 66 and 92% of the ground surface of two old-growth stands in northern Colorado (Veblen et al. 1991a). Most of these blowdowns occurred in winter when branches were snow covered and wind speeds were greatest (maximum of 324 km/hr at a nearby alpine site; Glidden 1981, 1982 in Veblen et al. 1991a). Blowdowns were clustered by year or groups of years, and stands 10-15 km distant exhibited similar blowdown dates, indicating windstorms may be regional events.

Studies of a subalpine blowdown covering >100 km², where wind speeds were estimated at 200-250 km/hr, revealed that the impact was variable across the landscape and was related to stand structure, composition, fire history, elevation, and topographic position (Veblen et al. 2001, Baker et al. 2002, Kulakowski and Veblen 2002). Damage was positively related to stand density, tree height, elevation, and higher slope position. Subalpine fir exhibited the highest rates of snapping, and quaking aspen suffered much less damage than conifers.

Pests and Pathogens - Bark beetles are important disturbance agents in Spruce-Fir Forests in the Southwest, with different species affecting different tree species (Alexander 1987, Dahms and Geils 1997) (see *Overview*). Western spruce budworm can impact both Engelmann spruce and subalpine fir (Alexander 1987), but in the Southwest it affects mostly white fir and Douglas fir (Moir 1993, Dahms and Geils 1997) and therefore has more impact on stands near the transition with Mixed Conifer Forest. Among pathogens, the most common are wood-rotting fungi, with basal decay occurring in old wounds and frost cracks (Alexander 1987), and root diseases (Dahms and Geils 1997).

Multiple studies indicate that spruce beetles have had the greatest impact in the Southwest and Colorado of any pest or pathogen affecting Spruce-Fir Forest. Outbreaks have occurred throughout recorded history (Alexander 1987). Old photographs and tree-ring analysis revealed six major outbreaks in the southern Rocky Mountains since the middle 1800s, and between the 1850s and 1880s an outbreak affected forests from central New Mexico northward to at least north-central Colorado (Baker and Veblen 1990), likely affecting stands in BAND. An outbreak from 1939 to 1951 impacted most subalpine forests in central-western and northwestern Colorado (Hinds et al. 1965, Veblen et al. 1991b), killing 99% of Engelmann spruce >25 cm dbh in some areas (Schmid and Frye 1977). Northern New Mexico was affected by large outbreaks in the 1970s (Dahms and Geils 1997), possibly impacting stands in BAND.

These and smaller outbreaks are considered natural in the region. Spruce beetle populations likely persist in areas of small windthrows (Schmid and Frye 1977, Veblen et al. 1991, Schmidt and Amman 1992) and in scattered live trees (Veblen et al. 1994). Such populations are kept at low levels by nematodes, insect parasites, and insect predators such as woodpeckers (Alexander 1987). Large population outbreaks are favored by predominance of Engelmann spruce in the canopy, high stand basal area concentrated in older, larger diameter Engelmann spruce, single or two-storied stands, slow diameter growth, mild winters, and well-drained creek-bottom sites (Schmid and Hinds 1974, Schmid and Frye 1977, Veblen et al. 1994). The frequency of spruce beetle outbreaks depends on size of the area, proportion of the area affected by recent outbreaks, and rate of stand growth into susceptible conditions (Schmid and Amman 1992). Despite knowledge of factors affecting outbreaks, prediction of outbreaks is difficult (Schmid and Amman 1992). A recent stand-scale modeling effort indicated that fire history was

the best predictor of beetle outbreak (areas recently burned had less chance of outbreak), but that dominance of nearby stands by Engelmann spruce and elevation were two other important predictors (Bebi et al. 2003).

In a study area of about 600 ha of mostly Spruce-Fir Forest in northwestern Colorado, 39% was affected by spruce beetle since about 1633 (Veblen et al. 1994). Mean return interval for spruce beetle outbreaks was 117 years, and turnover time was 259 years. Compared to 202 and 521 years, respectively, for fire, these intervals suggest that spruce beetles are at least as important as fire in the disturbance regime of some Spruce-Fir Forests in Colorado, a conclusion also reached by Baker and Veblen (1990) and Veblen et al. (1991b).

Interactions among disturbance agents - There are many important interactions among fire, wind, and spruce beetles.

As noted above, small, scattered windfalls appear to aid in maintaining small, persistent populations of spruce beetles (Schmid and Frye 1977, Veblen et al. 1991a, Schmid and Amman 1992). Larger blowdowns may trigger spruce beetle outbreaks (Schmid and Hinds 1974, Schmid and Frye 1977, Alexander and Shepperd 1984, Veblen et al. 1989, Veblen et al. 1994).

In turn, spruce beetle outbreaks potentially enhance fire by producing dead fuels (Martin and Mitchell 1980 in Dahms and Geils 1997), with fire danger greatest during the first few years after outbreaks when the trees retain dead needles and fine twigs (Schmid and Frye 1977). One early observer wrote "There has been a most intimate interrelation of destructive bark beetles and forest fires in the denudation of the vast areas of once heavily forested lands in the Rocky Mountain region, and that in very many cases the insects have first killed the timber, and the fire has then followed" (Hopkins 1909 in Baker and Veblen 1990).

The relationship between beetles and fire was challenged by Schmid and Hinds (1974), who concluded, "Although the beetle-killed snags are potential lightning rods and the massive number of dead trees has created a large fuel buildup, the fire hazard seems overexaggerated." More recent research indicated that it is difficult to assess whether spruce beetles increase the probability of fire (Baker and Veblen 1990), and one attempt to do so in Colorado found that areas impacted by a spruce beetle outbreak were not more susceptible to subsequent fires (Bebi et al. 2003).

Interactions among disturbances also include negative feedback. For example, crown fires lessen the potential for spruce beetle outbreaks (Bebi et al. 2003). In fact, outbreaks of spruce beetles are unlikely for approximately 70 years after crown fire, because Engelmann spruce must grow into the minimum diameter impacted by beetles (Veblen et al. 1994).

Interactions between wind and fire also occur, as wind damage is less in younger, more recently burned stands (Kulakowski and Veblen 2002). This relationship is clearer in areas of low- to moderate-severity blowdowns than in high-severity blowdowns. The interaction of fire and wind lasts for centuries.

Although it is generally assumed that Euro-American influence has had little impact on the disturbance regimes of Spruce-Fir Forest (e.g., Dahms and Geils 1997), even modestly effective fire exclusion may have reduced surface and mixed-severity (patch) fires and thereby increased changes, not only of large-scale crown fires, but also wind blowdowns and spruce beetle outbreaks.

Vegetation Dynamics

Fire, wind, spruce beetles, and root pathogens result in disturbances across a variety of scales, from small gaps or patches to large stands (Peet 1981, Veblen et al. 1991a, Rebertus et al. 1992, Dahms and Geils 1997); however, the impacts of these disturbances on vegetation dynamics can be quite different, even at the same scale. In fact, "type of disturbance appears more important than scale of disturbance in these forests" (Veblen et al. 1991a). The key difference among disturbances is whether mineral soil is exposed. Fire exposes mineral soil, but other disturbances do not, at least not to the same extent.

Little research has been done on succession in Spruce-Fir Forest in the Southwest. While much research has been carried out further north in the Rocky Mountains, findings do not always apply to the Southwest because lodgepole pine (*Pinus contorta*), a common pioneer species following crown fires throughout much of the Rocky Mountains is absent from Arizona and New Mexico.

Following stand-initiating fire in the Southwest (and in some stands further north), the pioneer trees are either Engelmann spruce, quaking aspen, or both (Whipple and Dix 1979, Veblen 1986a, Veblen et al. 1991a, Moir 1993). Engelmann spruce is more common at high elevations and in more mesic sites, while quaking aspen is more likely at lower elevations, along with white fir, Douglas fir, and blue spruce (Whipple and Dix 1979, DeVelice et al. 1986, Veblen 1986a, Moir 1993). Fire exposes mineral soil and Engelmann spruce germinates and establishes better on mineral soil or mixed mineral soil and humus than does subalpine fir (Knapp and Smith 1982), because soil moisture conditions are more consistent (Alexander and Shepperd 1984). Establishment success varies according to burn severity, ash depth, and exposure of mineral soil (Alexander and Shepperd 1984).

Subalpine fir also germinates and establishes on mineral soil as well as on moist humus (although it establishes better with shade and does well with less light than Engelmann spruce) (Alexander et al. 1984). Therefore, subalpine fir may co-establish with Engelmann spruce or follow several decades later (Veblen 1986a, Aplet et al. 1988, Rebertus et al. 1992, Patten and Stromberg 1995). The temporal and spatial pattern of colonization is strongly affected by the size of the burned area and the location of seed sources relative to prevailing winds (Peet 1981), as well as by site conditions.

Where quaking aspen is the primary pioneer species (establishing by sprouting of remnant root systems), it dies out after about 150 years (Moir 1993) as it is replaced by Engelmann spruce and subalpine fir (Merkle 1954).

Young Spruce-Fir Forests are generally free of disturbance for several decades. Re-occurring fire is unlikely because of low fuel loads, wind has little impact on small trees, and spruce beetles do not attack young trees. After perhaps 70 years of spruce growth, spruce beetles have the potential to infest stands (Veblen et al. 1994); however, the probability of an outbreak is small compared to old-growth stands. The probability of crown fires and spruce beetle outbreaks increases with time. Without large-scale disturbance, Engelmann spruce increases in canopy dominance, while subalpine fir increases in abundance in the understory (Aplet et al. 1988), in part because it establishes better on forest litter than does Engelmann spruce (Knapp and Smith 1982).

If stands remain free of stand-initiating disturbance for perhaps 300 years, the large, old canopy trees become susceptible to fine-scale windthrow disturbance (related to pathogenic root fungi and, on some sites, shallow root systems); therefore, canopy gap dynamics (single tree-scale succession) becomes increasingly important (Aplet et al. 1988, Veblen et al. 1991a). Although Engelmann spruce may be more abundant in the canopy, subalpine fir accounts for more treefalls as a result of greater susceptibility to root pathogens and perhaps a shorter life span (Schmid and Hinds 1974, Veblen 1986b, Alexander 1987). Subcanopy Engelmann spruce and subalpine fir are released and show similar growth responses in gaps. However, because subalpine fir is more common than Engelmann spruce in the subcanopy, it tends to have greater recruitment into gaps. The net result is that the longer life span of Engelmann spruce is counterbalanced by the greater abundance of subalpine fir and, as a result of these differences in life-history characteristics; the two species continue to co-dominate old-growth stands (Veblen 1986b, Veblen et al. 1991a). Therefore, wind does not differentially favor Engelmann spruce or subalpine fir.

Succession following large-scale windthrow and spruce beetle outbreaks differs from post-fire succession (Veblen 1991a). Crown fires kill trees of all sizes and expose mineral soil leading to germination and establishment of new individuals of Engelmann spruce and subalpine fir. In contrast, large scale windthrow and spruce beetle outbreaks kill primarily larger, older trees and leave the litter layer largely intact. After disturbance, subcanopy trees are released and both Engelmann spruce and subalpine fir grow into the canopy and continue high growth rates for 40 to >100 years (Veblen et al. 1994). In the absence of additional large-scale disturbance, small-scale gap dynamics eventually become important in these forests too. Reoccurring beetle outbreaks would lead to wave-like oscillations of greater and lesser

basal area of Engelmann spruce accompanied by oscillations of lesser and greater basal area of subalpine fir (Schmid and Hinds 1974).

Composition and Structure

There is a wide diversity of Spruce-Fir Forests in at least New Mexico (Moir 1993). Extensive research efforts have been made to classify them and describe their floristics (e.g., Moir and Ludwig 1979). New Mexico Spruce-Fir Forests also have considerable plant and animal endemism, which is related to the isolation of different areas of Spruce-Fir Forest in high elevation areas with Holocene warming (Moir 1993).

Less information is available on the diversity of Spruce-Fir forests in Arizona, but given that they occur over only about 30% as much land area, it is likely that Spruce-Fir Forests are less diverse in Arizona than in New Mexico. Also, given that there are fewer locations with Spruce-Fir Forest in Arizona than New Mexico (cf. Alexander 1987) it is likely that endemism is less common at the state-wide scale, but present within individual locations.

Trees

In general, tree height in the Spruce-Fir forest is >25 m, and stands may be layered with two or more age classes (Pase and Brown 1994b). Engelmann spruce and subalpine fir dominate at higher elevations, while quaking aspen, white fir, Douglas fir, and blue spruce occur at lower elevations, along with occasional ponderosa pine (Moir 1993, Pase and Brown 1994b). The presence of these species may reflect pre-1900 fires (Moir 1993) or may reflect a transition with Mixed Conifer Forest. The highest abundance of blue spruce is in canyons and along meadow margins (White and Vankat 1993, Pase and Brown 1994b).

In general, Engelmann spruce dominates subalpine fir in the canopy of old-growth undisturbed stands, in part because it may have a larger maximum size and longer life span (Alexander 1987). In contrast, subalpine fir predominates in smaller size classes, in part because it is more shade tolerant.

Several studies describe Spruce-Fir Forest of GRCA, both qualitatively (Merkle 1954) and quantitatively (White and Vankat 1993, Fulé et al. 2002b). Estimates of mean canopy cover are about 50%, but the range for individual stands is about 20 to 85%. Estimates of mean tree density range from 950 trees/ha (trees >2.5 cm dbh) to 1,400 trees/ha (trees > 1m height). Mean basal area has been estimated as 28-41 m²/ha. Generally, Engelmann spruce has the greatest relative basal area and density, followed by quaking aspen or subalpine fir. Both Engelmann spruce and subalpine fir grow below canopies of quaking aspen, reflecting potential successional replacement of quaking aspen.

Several sources infer that the current structure and composition of Spruce-Fir Forest approximate that present prior Euro-American influence (White and Vankat 1993, Dahms and Geils 1997). The reasoning is that the period of fire exclusion has been shorter than the fire interval, at least for crown fires (White and Vankat 1993) or that stands have been little affected by grazing by domestic livestock and fire exclusion (Dahms and Geils 1997). While likely true in comparison to Mixed Conifer and Ponderosa Pine Forests), such conclusions may be somewhat misleading.

Wherever fire exclusion has been effective in or near Spruce-Fir Forests, there would be fewer or smaller early successional stands, particularly in lower elevation areas. In young stands, the replacement of quaking aspen by Engelmann spruce and subalpine fir would have accelerated without surface and mixed-severity fires (Moir 1993). Older Spruce-Fir stands also would have changed, with greater fuel loads present today. In addition, more old stands would be present.

Forest reconstruction of 1880 conditions for an area of GRCA suggests that mean basal area has increased 168% (10 to 27.8 m²/ha) since 1880 and mean density has increased 531% (150 to 946 trees/ha) for trees >2.5 cm dbh (Fulé et al. (2002b). Spruce (Engelmann and blue spruce combined) increased in both relative basal area and density, while Douglas fir and quaking aspen decreased. Presumably, if the dates being compared involved different succession phases, findings would be very different.

Shrubs and Herbs

Understory cover may be high in young stands of Spruce-Fir Forest after canopy-removing disturbance (Yeager and Riordan 1953, Dye and Moir 1977, Moir 1993, Pase and Brown 1994b), but with increasing tree cover, there is a decline in shrub and herb cover. Estimates of mean understory shrub and herb cover in GRCA have been 15% (range of 3-25%) (White and Vankat 1993) and 25% (Fulé et al. 2002b). Litter has much greater cover (59%) and a mean depth (litter and duff combined) of 3.1 cm. Generally, understory cover is greater with lower canopy cover (Merkle 1954, Hurst 1977) and with greater soil moisture (Merkle 1954, Pase and Brown 1994b, Peet 2000).

Little information is known on changes in understory species since Euro-American settlement, other than what can be projected with changes in canopy cover. Leiberg et al. (1904) provided a species list of the herbaceous layer of Mixed Conifer and Spruce-Fir forests in an area of northern Arizona, but at least the Spruce-Fir area had been burned an estimated 100-110 years earlier and likely had been grazed by domestic livestock. Other species lists are available (cf. Moir 1993, Pase and Brown 1994b).

Animals

The New Mexico Department of Fish and Game maintains a searchable website (<http://nmmhp.unm.edu/bisonm/bisonquery.php>) which lists animal taxa for Spruce-Fir Forest in New Mexico and Arizona. Currently, the site lists 10 molluscs, 4 amphibians, 2 reptiles, 85 birds, and 111 mammals, fewer in each category than any other forest ecosystem considered in this report. Of course many of the taxa have ranges that extend outside the Spruce-Fir Forest. Amphibians and reptiles are few in number because of the cold climate (Pase and Brown 1994b).

Little information is available on the history of most species (Dahms and Geils 1997), but the New Mexico Department of Fish and Game considers some of the taxa listed on their website as extirpated and extinct. All six extirpated species and the one extinct species of the Spruce-Fir Forest are mammals.

Anthropogenic Stressors

There is a paucity of information on anthropogenic stressors potentially affecting the Spruce-Fir Forest of the Southwest. The information on fire exclusion is speculative. Few data on exotic species are available (exotic plants have a cover of 0.2% in GRCA and nearly all of it is Kentucky bluegrass with some dandelion; Fulé et al. 2002b). Possible ozone phytotoxicity has been mentioned, but primarily for stands near urban areas (Dahms and Geils 1997). Even visitor use is an unlikely stressor because of the remoteness of most stands of Spruce-Fir Forest in SCPN.

Figure 10. Ecosystem characterization model of Spruce-Fir Forest. Symbols are as follows: rectangles = biotic components, ovals = interactive controls, solid rounded rectangles = state factors, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships. Numbers next to relationships are keyed to [Table 5](#).

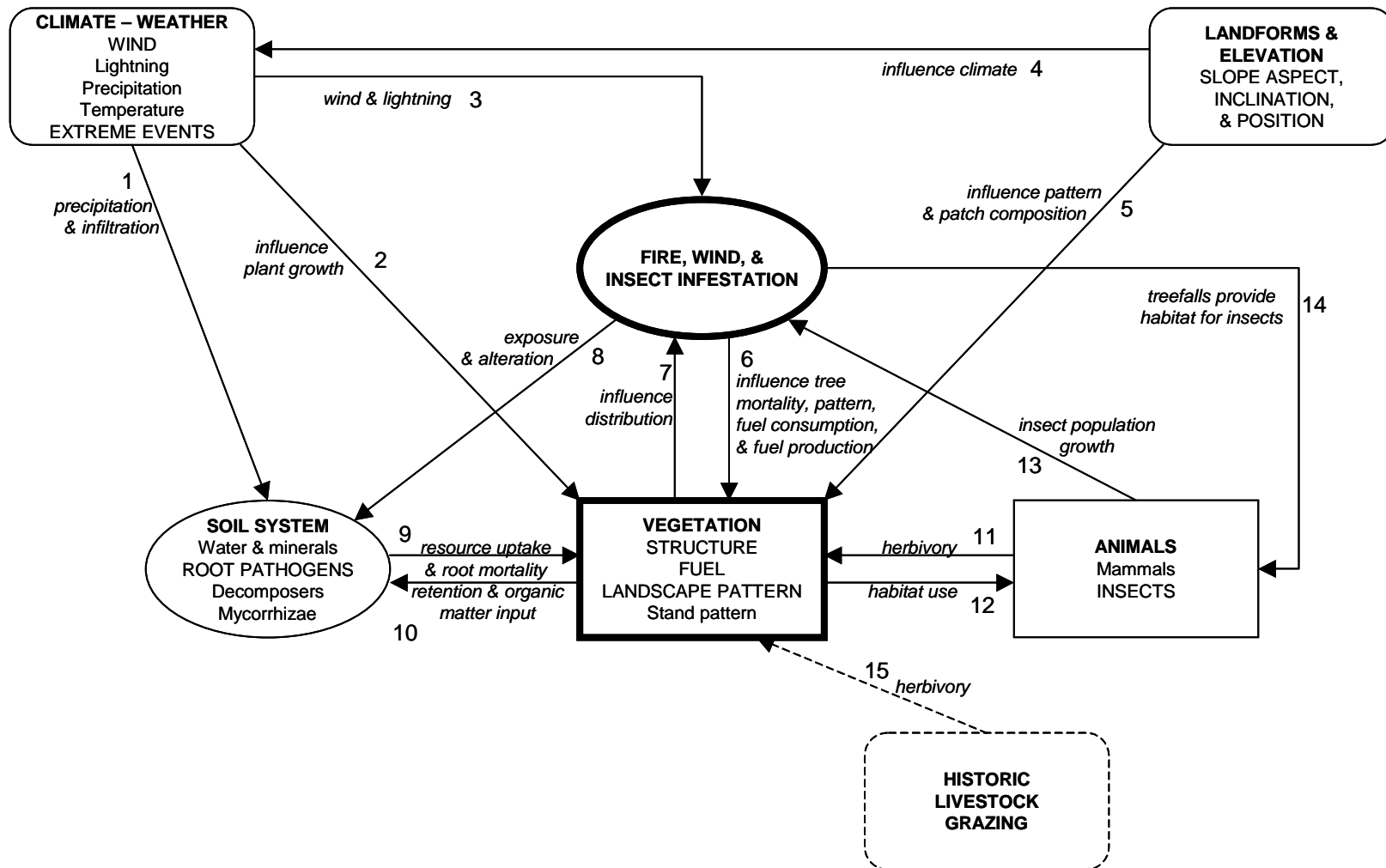


Table 5. Explanation of relationships shown in ecosystem characterization model of Spruce-Fir Forest. Numbers for relationships are keyed to [Figure 10](#).

Relationships	Circa 1880	Today
1	Precipitation & infiltration add to soil moisture. Snowmelt of winter snowpack is critical in recharging soil moisture (see text details).	Same
2	Climate is major factor determining plant growth.	Same
3	Wind causes blowdowns, and lightning ignites fires.	Same
4	Landforms influence microclimate and location of blowdowns. Elevation affects precipitation and evapotranspiration.	Same
5	Variation in landforms contributes to somewhat heterogeneous vegetation pattern in which tree densities differ among and within stands.	Same
6	Wind and spruce bark beetle infestations kill larger trees and reinforces the somewhat heterogeneous vegetation pattern. Crown fires kill trees in all size classes and produces a more homogeneous pattern (see text for details).	Same
7	Somewhat heterogeneous vegetation pattern results in somewhat heterogeneous wind and insect infestation pattern but has little effect on crown fire pattern.	Same
8	Blowdowns expose mineral soil. Crown fires expose soil surface and alter soil properties.	Same
9	Water and minerals in soil are absorbed by plants. Root pathogens contribute to tree mortality.	Same
10	Plants stabilize soil and produce coarse woody debris and litter.	Same
11	Herbivores graze vegetation.	Same
12	Vegetation serves as habitat for animals.	Same
13	Population growth of spruce beetle leads to insect infestations.	Same
14	Tree falls provide habitat for spruce bark beetle.	Same
15	Not applicable.	Historic livestock grazing likely reduced herb cover and changed species composition.

Figure 11. Ecosystem dynamics model of Spruce-Fir Forest. This model provides more detail on the vegetation - disturbance portion of the ecosystem characterization model (Figure 10) by showing the various communities (within different states) and processes that form them. Numbers next to relationships are keyed to Table 6.

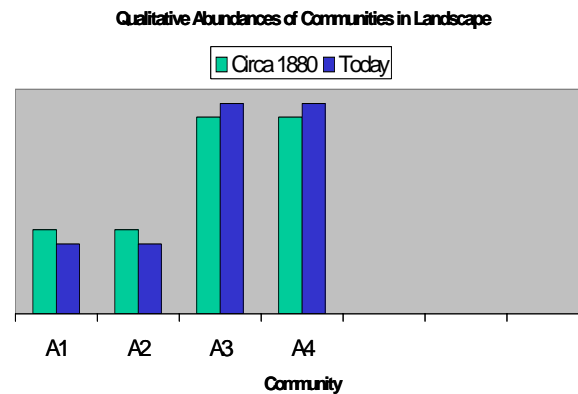
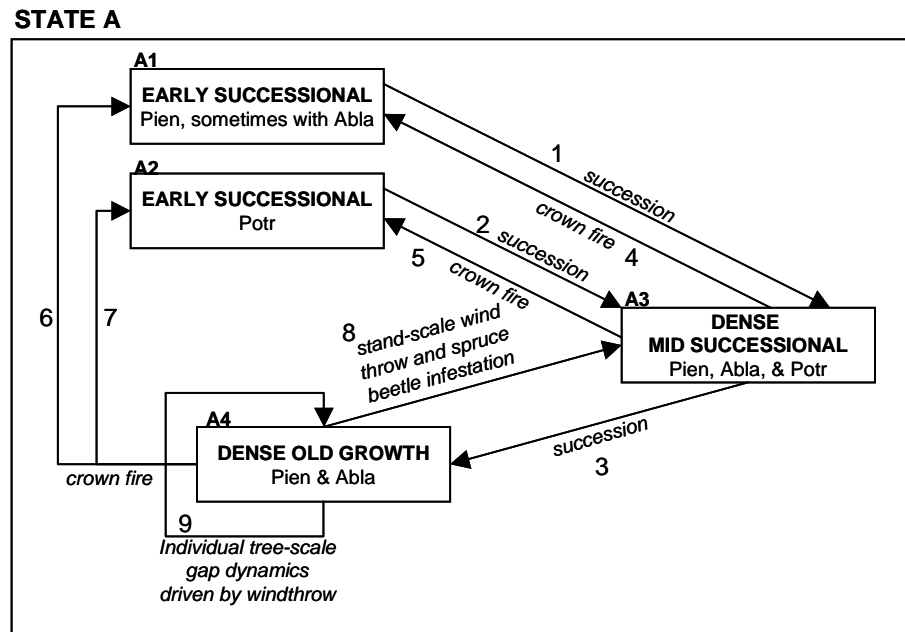
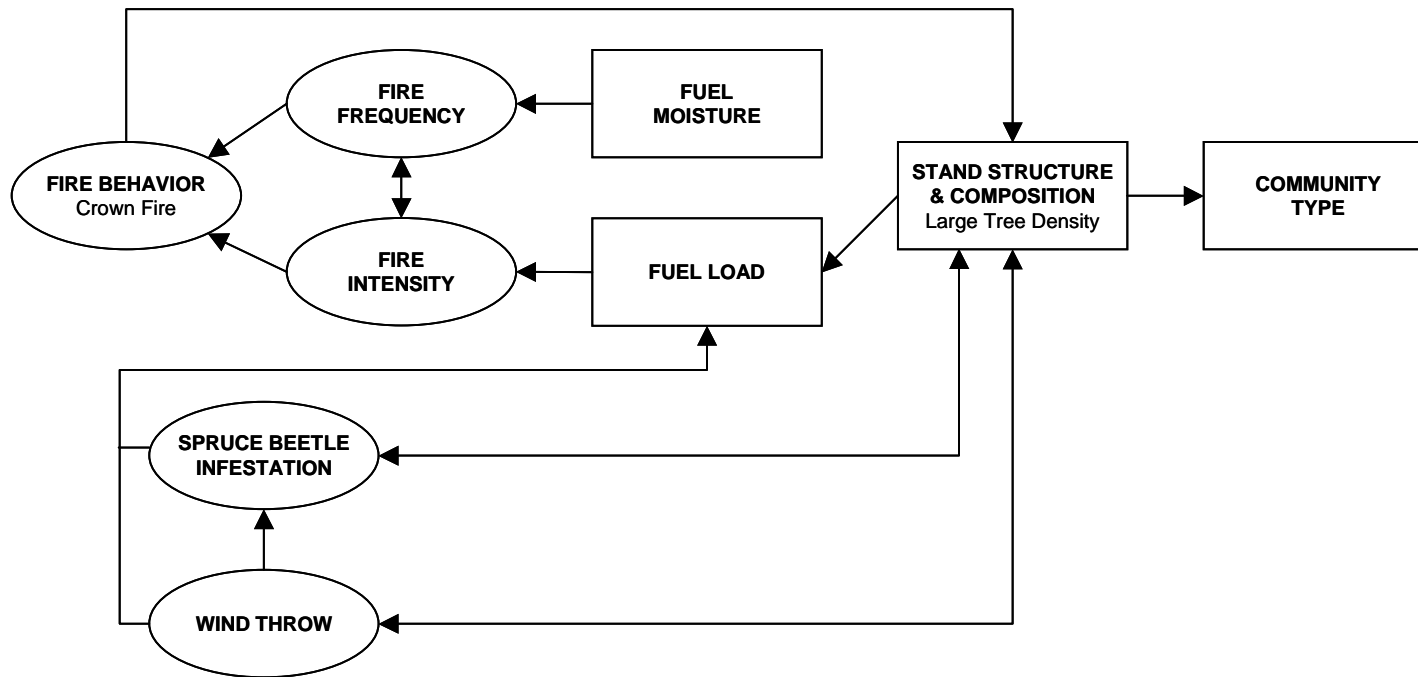


Table 6. Explanation of relationships shown in ecosystem dynamic model of Spruce-Fir Forest. Numbers for relationships are keyed to [Figure 11](#).

Relationships	Circa 1880	Today
1	In sites without quaking aspen, succession leads from early to mid successional stands.	Same
2	In sites with quaking aspen, succession leads from early to mid successional stands.	Same
3	Succession leads from mid successional to old-growth stands.	Same
4	Crown fire replaces mid successional stand, in which quaking aspen was absent, with early successional stand.	Same
5	Crown fire replaces mid successional stand, in which quaking aspen was present, with early successional stand.	Same
6	Crown fire replaces old growth in which quaking aspen was absent, leading to the establishment of an early successional stand of Engelmann spruce with some subalpine fir.	Same
7	Crown fire replaces old growth in which quaking aspen was present, leading to the establishment of an early successional stand dominated by quaking aspen.	Same
8	Stand-scale windthrow and spruce beetle infestation kills larger trees, returning old growth to mid successional stand.	Same
9	Treefalls of single to a few trees result in regeneration of trees that replace the original canopy tree(s) (see text for details).	Same

Figure 12. Mechanistic model of Spruce-Fir Forest. This model provides more detail on the mechanisms involved in the vegetation - fuel - disturbance interaction of the ecosystem dynamics model ([Figure 11](#)). Symbols are as follows: rectangles = biotic components, ovals = interactive controls, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships.



Montane Shrubland Ecosystem

Shrubland ecosystems, dominated mostly by 1-6 m tall deciduous shrubs of gambel oak, along with mountain mahogany, serviceberry, and others, are common in some areas of the Southwest. This ecosystem has been known by various names, including Petran chaparral and Great Basin montane scrubland, but is different from central Arizona's interior chaparral, which is dominated by evergreen shrubs (Brown 1994c). Within SCPN, stands of Montane Shrubland are widespread only in MEVE.

Given its limited distribution and low economic value, Montane Shrubland has been the subject of relatively little research (MacMahon 1988, Floyd et al. 2000). In fact it is often ignored or treated as a seral stage in forest succession (Brown 1994c). Given differences between northern and southern stands of this ecosystem (cf. Harper et al. 1985), this report focuses on literature from the Southwest and nearby regions.

Ecosystem Constraints and Drivers

Topography

Montane Shrubland occurs from 2,300-2,400 to >2,750 m in foothill and montane regions (Brown 1994c). Although it is extensive in some areas, in others it has a discontinuous distribution, occupying more xeric locations where soil moisture is less than the elevation and surrounding vegetation might suggest (Dick-Peddie 1993). Montane Shrubland is especially common on mountain slopes in southwestern Colorado (Brown 1994c), in the general vicinity of MEVE. Elsewhere it may occur as small stands (Dick-Peddie 1993).

Where Montane Shrubland is present it typically occurs between Pinyon-Juniper Woodland and Ponderosa Pine Forest. Because the Montane Shrubland shares species with both of these ecosystems, transitions can be broad, especially where there may be successional relationships between the Shrubland and the other ecosystems.

Climate

Few climate data are available from the Montane Shrubland (but see Brown 1994c, Harper et al. 1985). In general, the climate is characterized by cool to cold temperatures that produce a moderately long to short potential growing season that may be <100 days in some years. The range in mean annual precipitation is typically 380-535 mm and mean annual temperature is 7-10°C. Snowfall is sometimes blown off stands. As elsewhere on the Colorado Plateau, summer precipitation is abundant in the south and decreases northward (see *Overview*). Lightning is likely also an important component of the climate.

Inference suggests that the relatively low precipitation, coupled with poor soil development, limits the growth of coniferous forest trees on sites with Montane Shrubland (Brown 1994c). Low winter temperatures (which commonly drop below -6°C) also may limit growth of Pinyon-Juniper Woodland at these elevations. Montane Shrubland itself appears limited at lower elevations by water stress and at higher elevations by temperature-related factors and competition (Harper et al. 1985).

Soil

Montane Shrubland occurs on soils formed from a variety of parent materials (Harper et al. 1985). Soils are generally poorly developed because of the steep slopes (Brown 1994c), but have a high moisture holding capacity (Harper et al. 1985). Most of the soils in stands in southwestern Colorado are Mollisols (Argic Pachic Cryoborolls and Argic Cryoborolls) (Steinhoff 1981 in Harper et al. 1985). Such soils tend to be well-drained, moderately deep to deep, and gravelly but fine- to medium-textured (Hendricks 1985).

Fires appear to affect soils by reducing leaf litter and increasing pH, nitrogen, phosphorus, and potassium (Baker 1949 in Harper et al. 1985).

Stand-Scale Disturbance

Fire - Many stands of Montane Shrubland are highly flammable as a result of their dense structure, leaf litter, and continuous fuels from herbs that fill shrub interspaces (Floyd et al. 2000). Nevertheless, the fire

regime is little studied, except for stands in MEVE (cf. Floyd et al. 2000). Turnover time for a 6600 ha site in MEVE was about 100 years during the mid to late 19th century when Euro-American influence was small. The frequency of fires was greatly reduced in the first half of the 20th century, resulting in an increased estimated turnover time of about 200 years during this period. The major reason for the change in fire regime was likely generally moist conditions during this period (cf. Swetnam and Betancourt 1998), but reduction of fine fuels by livestock grazing and fire exclusion activities after the establishment of MEVE in 1906 also may have been important (Floyd et al. 2000). Surprisingly, despite continued efforts at fire exclusion involving more advanced technologies, the turnover time since the mid 20th century has returned to the 19th century figure of 100 years. This was likely the result of several summers with severe fire weather, augmented by the lack of grazing (Floyd et al. 2000).

Recent large fires in MEVE occurred with high winds and drought, mostly in late June and early July (Floyd et al. 2000), which is near the beginning of the monsoon season when fuels are dry and lightning becomes common. Most fires affecting Montane Shrubland originally ignite in stands of Pinyon-Juniper Woodland (Omi and Emrick 1980 in Floyd et al. 2000).

Pests and Pathogens - Although several insects are associated with gambel oak (Harper et al. 1985, Cranshaw et al. 1994), most do little damage. However, several years of defoliation by a looper (possibly *Lambdina punctata*) may kill stems (Brown 1958).

Vegetation Dynamics

The question whether the Montane Shrubland ecosystem is a seral or climax type has been debated (Brown 1958, Brown 1994c, Harper et al. 1985, Dick-Peddie 1993). It appears that in some locations, without reoccurring disturbance (i.e., fire), Montane Shrubland can be replaced by Pinyon-Juniper Woodland or Ponderosa Pine Forest. Even late in succession, shrubs of the Montane Shrubland may persist as understory species in these ecosystems (Dick-Peddie 1993). In other areas, climate or soils may preclude the invasion of conifers (Brown 1958).

In areas of reoccurring large fires, such as MEVE, the debate of seral vs. climax may be mute as Montane Shrubland is maintained by fire (Erdman 1970 in Floyd et al. 2000, Floyd et al. 2000). Large fires generally kill the above-ground parts of gambel oak and other species; however, many species, including gambel oak, mountain mahogany, and serviceberry, resprout prolifically following fire, and other species reestablish by seed (Floyd et al. 2000). In contrast, pinyon pine (*Pinus edulis*), some junipers (*Juniperus* spp.), and young ponderosa pine (*Pinus ponderosa*) do not respond as effectively to fire. Regeneration of Montane Shrubland species is so effective that shrub cover becomes similar to unburned stands within two years after fire (Floyd et al. 2000). After initial re-establishment, stands thin with time (Brown 1958).

Composition and Structure

Shrubs

Little is known about the Montane Shrubland prior to Euro-American influence. Shrublands lacked the obvious economic value that motivated many early descriptions of forests and grasslands, and shrublands also lack long-lived individuals that enable reconstruction of past structure and composition.

Early Euro-Americans in at least northern Utah and west-central Colorado wrote about forests and grass and occasionally mentioned the presence of oak-dominated shrublands (Christensen 1950, Brown 1958). These writings provide little information on the structure and composition of Montane Shrublands, but generally confirm that gambel oak was present in today's locations. One early description for west-central Colorado stated, "There are in the reserve low-lying brush-covered hills of vast extent, where, very probably, from the nature of conditions, forest trees have never existed and will never exist" (Sudworth 1900 in Brown 1958).

Livestock grazing became widespread in the Montane Shrubland (Brown 1958, Brown 1994c), and herders were reputed to have set fires (Brown 1958). It is commonly written that grazing, fires, and fire exclusion have increased the extent and density of stands (Brown 1958, Rogers 1982, West and Young 2000) and even influenced species composition (Harper et al. 1985). There is evidence for Utah of

stands having increased in area, having less open space among clumps of shrubs, and having invaded new sites (Christensen 1950, Rogers 1982). Excessive deer and elk grazing may have influenced stand structure and shrub regeneration (West and Young 2000). However, there is evidence of little change in some areas (Brown 1958), and the finding that today's fire regime in the Montane Shrubland of MEVE is similar to that before Euro-American influence (Floyd et al. 2000) suggests little change in at least stand structure, assuming that fire is a major driver of this ecosystem.

Today, Montane Shrubland stands in the Southwest range from dense, homogeneous shrub thickets to heterogeneous mixtures of clumps of shrubs and openings between them (Brown 1994c). The dense thickets tend to occur on steep slopes that may facilitate the spread of fires followed by dense resprouting, and heterogeneous clumps occur more commonly on gentle slopes (Brown 1958). Trees of pinyon pine, junipers, ponderosa pine, or Douglas fir may be scattered in stands (Brown 1994c, Floyd et al. 2000).

Shrub species composition is affected by several factors, including elevation, aspect, and soil (Steinhoff 1981 in Harper et al. 1985, Floyd et al. 2000). Areas of seeps and small water catchments have different species composition (Dick-Peddie 1993). Species lists are available (cf. Dick-Peddie 1993, Brown 1994c), as are details on species distributions (Dick-Peddie 1993).

Herbs

The characteristics of the herb layer of the Montane Shrubland before Euro-American influence became widespread are unknown. Presumably, the herb layer was at least as well developed as today.

Most of the native herbs present today also occur in other montane ecosystems and Great Basin grasslands (Brown 1994c). Livestock grazing reduced palatable herbs (Harper et al. 1985), especially grasses (Brown 1994c). Today, less-palatable forbs are common, as are non-native brome grasses and Kentucky blue grass (Brown 1994c). Species lists are available (Dick-Peddie 1993, Brown 1994c).

Animals

The New Mexico Department of Fish and Game maintains a searchable website (<http://nmmhp.unm.edu/bisonm/bisonquery.php>) which lists animal taxa for Montane Shrubland in New Mexico and Arizona. Currently, the site lists no mollusks, no amphibians, 24 reptiles, 96 birds, and 129 mammals, fewer in each category than the Ponderosa Pine Forest except for reptiles. In fact the Montane Shrubland has 38% more reptiles than any other ecosystem considered in this report. Of course many of the taxa have ranges that extend outside the Montane Shrubland.

Little information is available on the history of most species (Dahms and Geils 1997), but the New Mexico Department of Fish and Game considers some of the taxa listed on their website as extirpated and extinct. All five extirpated species and one of the two extinct species of the Montane Shrubland Ecosystem are mammals; the other extinct species is a bird.

Anthropogenic Stressors

Some sources indicate that fire exclusion is an anthropogenic stressor of the Montane Shrubland (Rogers 1982); however, this perspective is challenged by the finding that today's fire regime in the Montane Shrubland of MEVE is similar to that before Euro-American influence (Floyd et al. 2000). No other anthropogenic stressors are known or have been hypothesized to be significant

Figure 13. Ecosystem characterization model of Montane Shrubland. Symbols are as follows: rectangles = biotic components, ovals = interactive controls, solid rounded rectangles = state factors, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships. Numbers next to relationships are keyed to [Table 7](#).

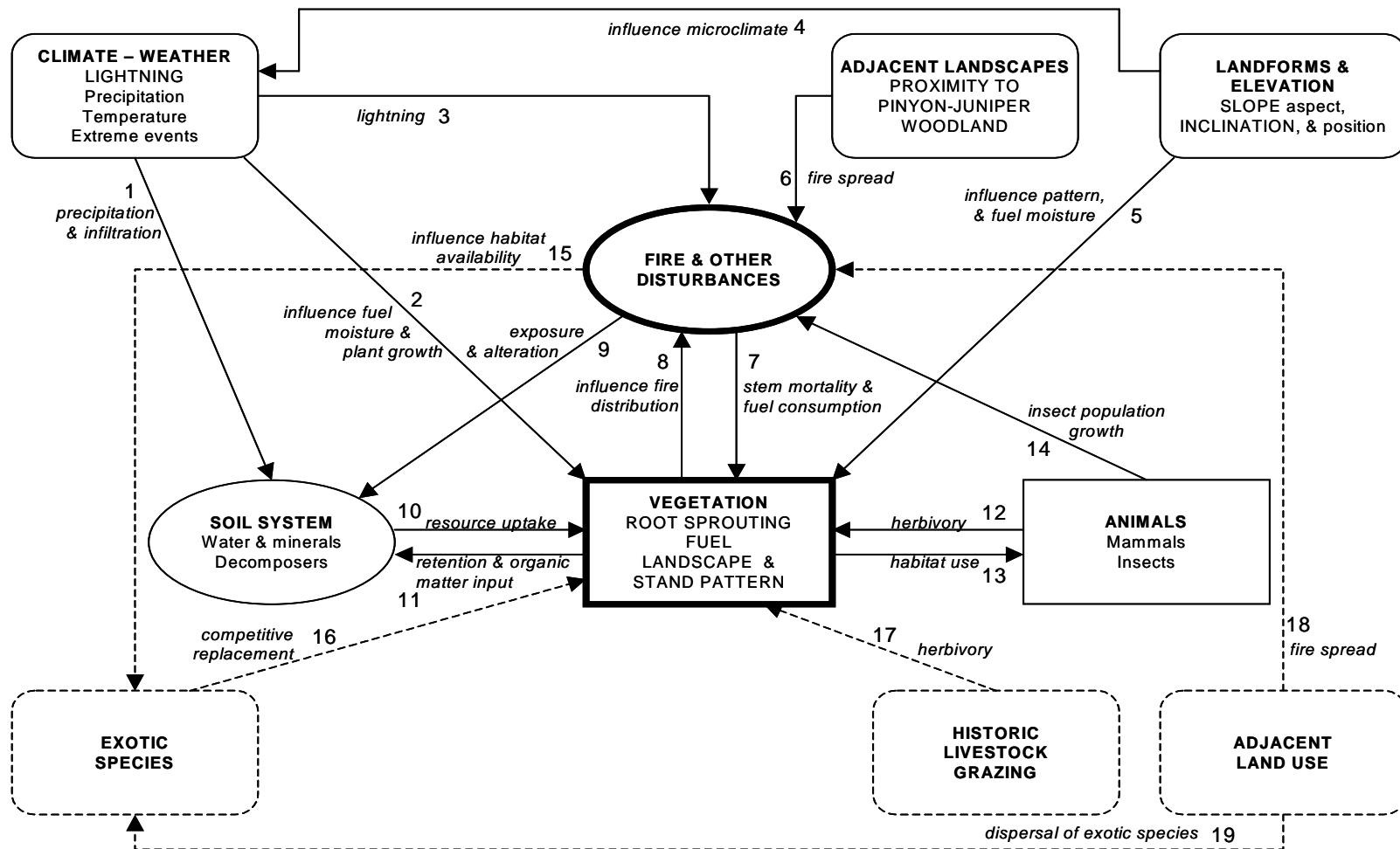


Table 7. Explanation of relationships shown in ecosystem characterization model of Montane Shrubland. Numbers for relationships are keyed to [Figure 13](#).

Relationships	Circa 1880	Today
1	Precipitation & infiltration add to soil moisture.	Same.
2	Climate is major factor determining plant growth.	Same.
3	Lightning ignites fires.	Same.
4	Landforms, especially slope inclination, result in microclimate variation.	Same.
5	Relatively homogeneous steep slopes result in relatively homogeneous landscape.	Same.
6	Fires spread into ecosystem from lower elevation Pinyon-Juniper Woodland Ecosystem.	Same.
7	Relatively homogeneous landscape pattern results in relatively homogeneous fire pattern.	Same.
8	Crown fires kill above-ground stems.	Same.
9	Crown fires expose soil surface and alter soil properties.	Same.
10	Water and minerals in soil are absorbed by plants.	Same.
11	Plants stabilize soil and produce coarse woody debris and litter.	Same.
12	Herbivores graze vegetation.	Same.
13	Vegetation serves as habitat for animals.	Same.
14	Population growth of insects leads to infestations.	Same.
15	Not applicable.	Disturbance inside SCPN units creates habitat for exotic species.
16	Not applicable.	Exotic species successfully compete with native species. Some exotics may have the potential to alter ecosystem processes.
17	Not applicable.	Historic livestock grazing reduced the herb cover and likely changed species composition.
18	Not applicable.	Human-caused fires originating outside SCPN units may spread into units.
19	Not applicable.	Disturbances outside SCPN units provide sites for establishment of exotic species, which are then more likely to be dispersed into the units.

Figure 14. Ecosystem dynamics model of Montane Shrubland Forest. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model ([Figure 13](#)) by showing the various communities (within different states) and processes that form them. Numbers next to relationships are keyed to [Table 8](#).

STATE A

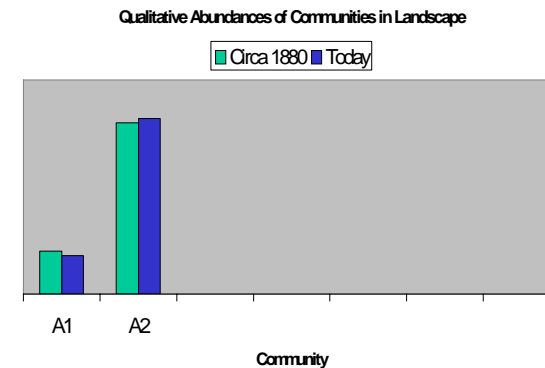
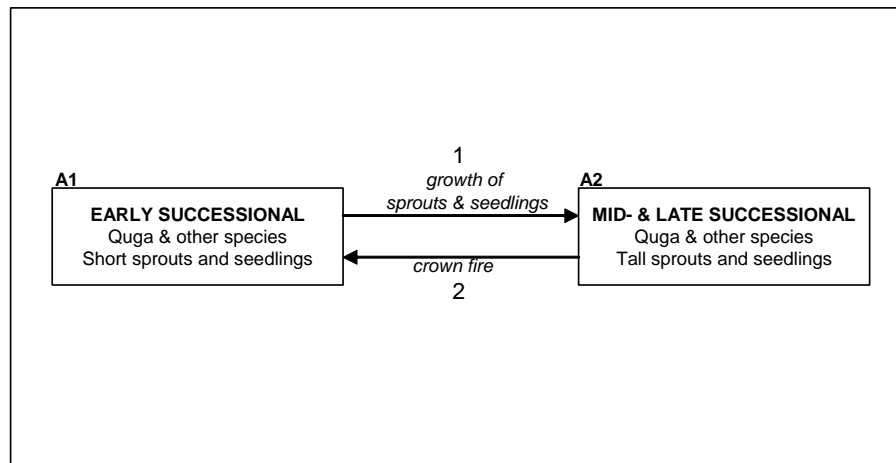
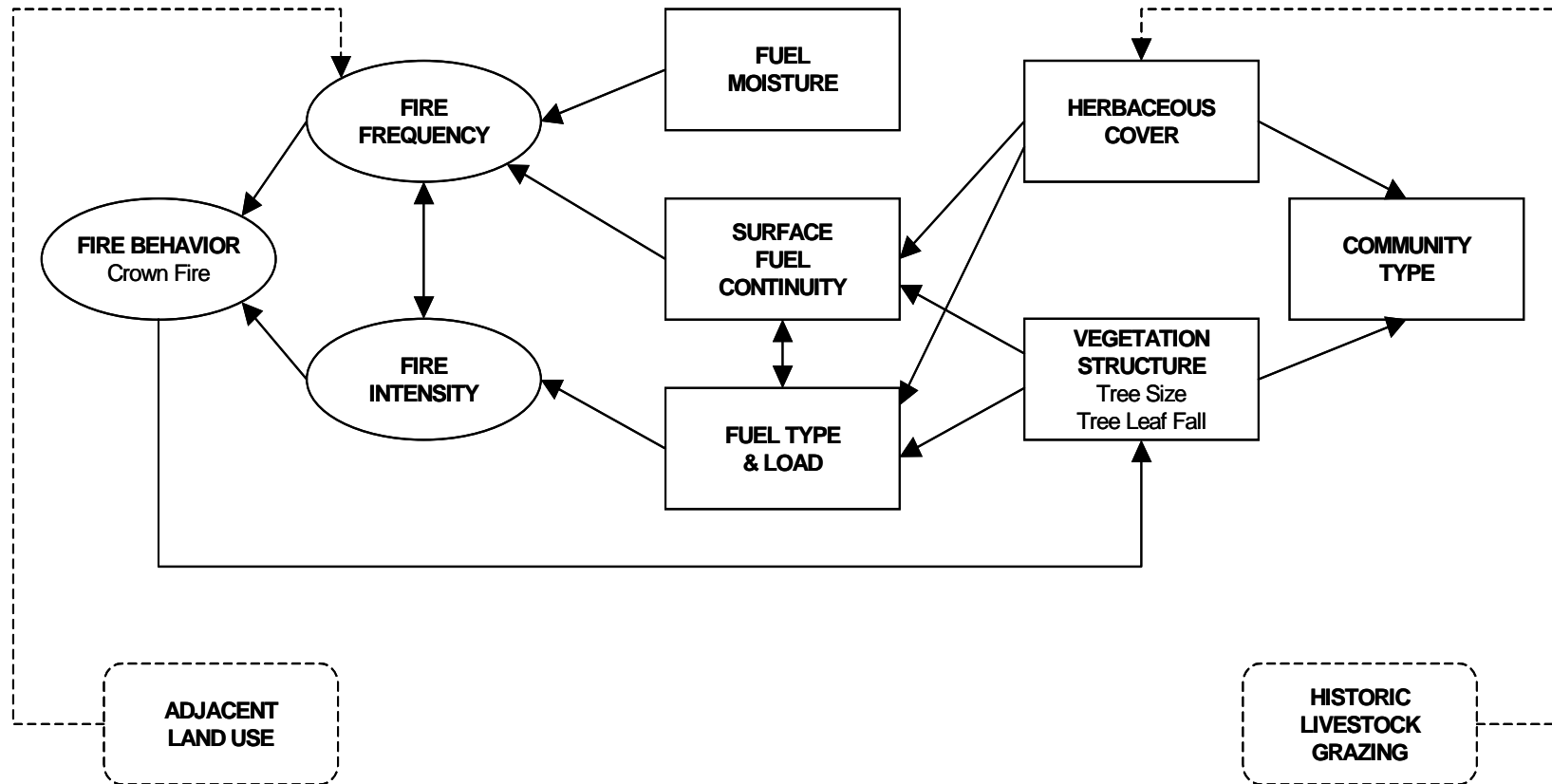


Table 8. Explanation of relationships shown in ecosystem dynamic model of Montane Shrubland. Numbers for relationships are keyed to [Figure 14](#).

Relationships	Circa 1880	Today
1	Post-fire stands are regenerated by a combination of root/crown sprouting and seeding. Growth of sprouts and seedlings leads to mid- and late-successional stands (see text for details).	Same
2	Crown fire kills above-ground stems, reinitiating regeneration.	Same

Figure 15. Mechanistic model of Montane Shrubland. This model provides more detail on the mechanisms involved in the vegetation - fuel - fire interaction of the ecosystem dynamics model (Figure 14). Symbols are as follows: rectangles = biotic components, ovals = interactive controls, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships.



Montane-Subalpine Grassland Ecosystem

Montane-Subalpine Grassland dominated by fescues (*Festuca* spp.), other grasses, and forbs occurs in areas from small meadows to large "parks" and mountainsides. Some authors separate grasslands based on montane vs. subalpine elevational zones (e.g., Brown 1994b); however, other authors combine the two (e.g., Dick-Peddie 1993). Review of the literature indicates that grasslands of the montane and subalpine elevational zones have many similarities and intergrade where differences occur. Given the absence of definitive data separating grasslands according to elevation, this report joins Dick-Peddie (1993) and others in combining the grasslands. In fact, the body of literature on grasslands suggests that classification of SCPN grasslands may be better based on site conditions (bottomlands and gentle slopes vs. steep slopes; [Figure 1](#)).

There has been relatively little research on the Montane-Subalpine Grassland. Stands occur throughout the Rocky Mountains, but there are regional differences (cf. Turner and Paulsen 1976, Peet 2000). Therefore, this report focuses on literature from the Southwest and nearby regions. Given uncertainties regarding classification of grasslands of SCPN, much of the information presented in this section is generic. Where there are clear differences among grasslands, information is separated.

Ecosystem Constraints and Drivers

Topography

Montane-Subalpine Grassland occurs nearly throughout the range of coniferous forests, from about 1,900 to 3,500m. Stands occupying valley bottoms and gentle slopes generally have a discontinuous distribution through the forest with most stands <100 ha (Rasmussen 1941, Dick-Peddie 1993, Brown 1994a, 1994b, Peet 2000). Other stands occur on expansive, relatively steep, south-facing slopes, particularly above 2745 m in the Jemez Mountains (including BAND) of northern New Mexico (Allen 1984, 1989).

Climate

There are little or no climate data for the Montane-Subalpine Grassland of the Southwest, but presumably the climate is similar to that of the surrounding forests. In general, summers are relatively cool and winters cold. Mean annual precipitation has been estimated as 360-1,150 mm for grassland in the subalpine zone (Brown 1994a), and precipitation in the montane zone is likely to average near the lower end of this range. *Festuca*-dominated grasslands in Colorado receive 610 mm precipitation (Weaver 1979). The percentage of precipitation falling as snow likely increases with higher elevation, with grassland in the subalpine zone receiving 50-75% as snow, which in valley bottoms and gentle slopes commonly builds up to depths of 1.8 m and covers stands from October through May (Turner and Paulsen 1976). Snow buildup is much less for stands on steep, south-facing slopes (Allen 1984). The growing season is short, especially in the subalpine zone where it is often <100 days (Brown 1994a), and summer frosts occasionally occur (Turner and Paulsen 1976). Mountain grasslands in Colorado have mean temperatures for the coldest and warmest months of -10 and 14°C, respectively (Weaver 1979).

In comparison to surrounding forests, the microclimates of Montane-Subalpine Grassland in valley bottoms and on gentle slopes appear to have generally cooler minimum and maximum temperatures, at least in summer and early fall (Rasmussen 1941, Brown 1994a). Evaporation rates may be higher than in the forests, as well as higher in grasslands in the montane zone vs. the subalpine zone (Brown 1994a).

Soil

Montane-Subalpine Grasslands in valley bottoms and on gentle slopes occur on finely-textured alluvial or colluvial soils (Peet 2000). Soils are variable, but most are deep, well-developed, and well-drained (Warren et al. 1982, Brown 1994a). The deep snowpack maintains soil temperatures at or above freezing during the winter and saturates the soil in the spring (Turner and Paulsen 1976). Soils resemble prairie soils with a deep, dark, organic A horizon (Moir 1967, Turner and Paulsen 1976). Most are Alfisols or Mollisols, but some are Entisols (Maker and Saugherty 1986). In comparison to surrounding forests, these soils tend to be finer textured, deeper, and less well drained (Turner and Paulsen 1976), as well as to have greater soil moisture in the summer (Merkle 1953). The fine texture is likely an important factor in

the distribution of these grasslands, especially in the montane zone, but is less important in the subalpine zone where excessive soil moisture may be keys along with cold-air drainage, frost pockets, deep snow, etc. (Peet 2000). Moir and Ludwig (1979) considered meadows dominated by Thurber fescue (*Festuca thurberi*) in Arizona and New Mexico as edaphic climaxes on fine-textured soils, possibly as relicts of warmer or drier post-glacial climates.

Stands on steep slopes in the Jemez Mountains occur on Mollisols (largely Pachic Cryoborolls and Pachic Paleborolls) that have deep profiles of 1.5m or more and sharply differ from the Alfisols and Inceptisols of adjacent forests (Allen 1984). The grassland soils are not moist, but are well-drained.

Little is known about the effects of disturbance, particular fire, on Montane-Subalpine Grassland soils. Presumably, fire reduces litter and soil moisture and increases soil temperature and nutrient availability. Grazing appears to increase soil temperatures and decrease soil moisture and fertility (Turner and Paulsen 1976).

Stand-Scale Disturbance

Fire - Review of the literature indicates that the effects of fire on Montane-Subalpine Grassland, at least in valley bottoms and on gentle slopes, are poorly known (cf. Turner and Paulsen 1976). Fire probably was not a cause of these grasslands, at least on the Kaibab Plateau (Rasmussen 1941), but fires likely formerly restricted tree invasion into grasslands in GRCA (Moore 1994) and are considered important in stands at low elevation (Dick-Peddie 1993). In addition to deterring trees from invading stands, fire possibly may affect species composition within stands, especially the abundance of shrubs (Turner and Paulsen 1976).

Fire was likely at least as important in grassland stands on steep slopes (cf. Allen 1984). This can be inferred from the landscape setting of dry, expansive slopes where clumps of trees are generally restricted to the upslope and lee side of topographic breaks. Also, ridgetops are sites of abrupt transition from grassland on drier slopes to forests on mesic slopes. Additional evidence of fire is that relict trees in ecotones surrounding grassland stands often are fire-scarred. It is estimated that fires formerly occurred in these grasslands every 15 years or less (Allen 1984).

Animals - Montane-Subalpine Grassland is utilized by grazers such as deer, elk, pronghorn antelope, and burrowing animals such as pocket gophers (Turner and Paulsen 1976). Extraordinary grazing by any of these native grazers would affect species composition by reducing palatable species and increasing less palatable species (e.g., Wolters 1996 for BAND). Excessive deer grazing is likely to have dramatically altered the ability of quaking aspen to invade meadows of GRCA in the 1920s and early 1930s (Moore 1994). In addition, burrowing animals are important in aerating the dense soil (Turner and Paulsen 1976) and may provide sites of mineral soil where competition is low for germinating seeds.

Vegetation Dynamics

Review of the literature revealed no information on succession or other vegetation dynamics following natural disturbance. In addition, little is known about the recovery of stands after livestock grazing, because (a) there is little information on the original composition of stands, (b) stands outside preserves continue to be grazed, and (c) grazing was so disruptive (including facilitating the establishment of exotic species) that full recovery may be impossible. In a comparison of stands inside and outside of the North Rim portion of GRCA, stands inside the Park (where livestock grazing had ended 20-30 years earlier) had "considerably" greater cover of grasses (Merkle 1953). A later report stated that total plant cover averaged 42% inside the Park and 35% outside (Merkle 1962).

Composition and Structure

Herbs, Trees, and Shrubs

Little is known about the Montane-Subalpine Grassland prior to Euro-American influence, other than stands were present in areas where they occur today. One description of the Kaibab Plateau stated, "There is a constant succession of parks and glades--dreamy avenues of grass and flowers winding between sylvan walls, or spreading out in broad open meadows" (Dutton 1882). In the Jemez Mountains of northern New Mexico, some of the mountains were named by early Spaniards for grasslands: Cerro

Pelon = bald peak and Cerro Pelado = baldy peak.

Two aspects of Euro-American land use likely had large impacts on the Montane-Subalpine Grassland: livestock grazing and reduced fire frequency, both beginning in the second half of the 19th century. Long-lived, fire-scarred trees adjacent to grassland stands have the potential to reveal the fire regime (cf. Allen 1984, Moore 1994), but reconstructions of the composition of grassland vegetation have relied on observation of the effects of current livestock grazing. After reviewing the available literature, Turner and Paulsen (1976) speculated that Thurber fescue, a bunchgrass, dominated the vegetation of stands in the subalpine zone, with forbs abundant in disturbed sites and at higher elevations and shrubs abundant at lower elevations.

Today's stands, at least where protected from livestock grazing, are generally dominated by a mix of grasses and many species of forbs, along with some shrubs (see species lists in Turner and Paulsen 1976, Dick-Peddie 1993, Brown 1994a). Low elevation sites, such as in the montane zone, tend to be dominated by Arizona fescue (*Festuca arizonica*), while higher elevation sites, such as in the subalpine zone, are dominated by Thurber fescue. The dominant native grasses include bunchgrasses up to 1 m in height. Cover ranges from 35 to 100% in stands in valley bottoms and on gentle slopes in GRCA (Warren et al. 1982). Species composition reportedly varies stand to stand, and species can be restricted to one or a few sites within a region (Warren et al. 1982). On steep slopes in the Jemez Mountains, plant cover was 81%, with 43% grasses, 31% forbs, and 7% sedges (Allen 1984). Grasslands dominated by Thurber fescue are widely distributed in the West, from New Mexico to British Columbia (Allen 1984).

Species' distributions appear to be influenced primarily by soil texture, soil moisture levels, elevation, site exposure (e.g., ridges), and disturbance (Merkle 1953, Turner and Paulsen 1976, Warren et al. 1982, Dick-Peddie 1993, Brown 1994a). For example, wetter sites have sedges (*Carex* spp.) (Warren et al. 1982, Dick-Peddie 1993, Brown 1994a) in what has been called a wet meadow community (Turner and Paulsen 1976).

Exotic species such as Kentucky bluegrass are common, especially with grazing; however, stands appear to recover in a few years when grazing is reduced, although recovery is incomplete (Dick-Peddie 1993, Wolters 1996). Meadows in lowlands and gentle slopes in the Jemez Mountains commonly have exotics as dominants (Allen 1989).

Montane-Subalpine Grassland is also subject to invasion by trees (Moir 1967, Turner and Paulsen 1976, Allen 1984, Dick-Peddie 1993, Brown 1994a, Moore 1994). Prior to Euro-American influence, tree invasion was less frequent. However, at least low- and mid-elevation grasslands were fringed by open, savanna-like forest, and later these trees likely served as seed sources for invasion (Allen 1984). There is much conjecture on what factors limited tree establishment, and therefore what has caused meadows and parks to shrink in size with tree invasion (Moore 1994). Possible limiting factors in stands in valley bottoms and on gentle slopes include poor drainage, fine-textured soil, soil heaving, absence of necessary mycorrhizal symbionts, seasonal drought, long-term precipitation patterns, low temperatures including frost, fire, animal activity, and competition from herbs (Merkle 1962, Moir 1967, Turner and Paulsen 1976, Allen 1989, Moore 1994). Likely factors in stands on steep slopes are high fire frequency, dry conditions, absence of sources of seeds of drought-tolerant tree species, difficulty of tree seedling establishment through thick sod, and winter kill of tree seedlings (when water lost through transpiration could not be replaced from the frozen soil).

An extensive study of tree invasion of Montane-Subalpine Grassland in valley bottoms and on gentle slopes in the North Rim region of GRCA found that all canopy tree species (except Douglas fir) were invaders, but that most invaders were quaking aspen (58%), Engelmann spruce (18%), and white fir (10%) (Moore 1994). Tree ages indicated that invasions had been continuous or episodic since grazing began, but different species exhibited different temporal patterns of invasion. The mean rate of encroachment of all species at all sites was 0.34 m/yr, with a high of 0.45 m/yr for quaking aspen. Early encroachment likely occurred as a result of fire exclusion. Seasonal drought and other factors influence encroachment at the local scale, but climate events (i.e., El Niño-Southern Oscillation) and fire exclusion are keys at the landscape scale.

In the Jemez Mountains, stands on steep slopes have been invaded primarily by ponderosa pine and Douglas fir (even at elevations far above their normal range), as well as by quaking aspen and Engelmann spruce (Allen 1984, 1989). Invasion first became common in the 1920s, at the beginning of effective fire exclusion and a change in grazing from numerous sheep to fewer cattle. Tree seedling establishment is thought to have been especially common in the brief period between the end of intensive sheep grazing and the recovery of grassland vegetation cover. Fire exclusion aided the survival of newly established seedlings. Between 1935 and 1981, grassland area has been reduced by 55%, with several small stands having disappeared and larger stands being fragmented (Allen 1989).

Animals

The New Mexico Department of Fish and Game maintains a searchable website (<http://nmnhp.unm.edu/bisonm/bisonquery.php>) which lists animal taxa for Montane-Subalpine Grassland of New Mexico and Arizona. Currently, the site lists no mollusks, 2 amphibians, 7 reptiles, 72 birds, and 122 mammals. Of course many of the taxa have ranges that extend outside the Montane-Subalpine Grassland.

Little information is available on the history of most species (Dahms and Geils 1997), but the New Mexico Department of Fish and Game considers some of the taxa listed on their website as extirpated and extinct. All five extirpated species and the one extinct species of the Montane-Subalpine Grassland are mammals.

Anthropogenic Stressors

Fire exclusion is likely an anthropogenic stressor of Montane-Subalpine Grassland, facilitating tree invasion of stands (see above). In addition, invasions of exotic species occur. Historic livestock grazing may have facilitated erosion, including incised drainage in some stands in valley bottoms and on gentle slopes.

Figure 16. Ecosystem characterization model of Montane-Subalpine Grassland. Symbols are as follows: rectangles = biotic components, ovals = interactive controls, solid rounded rectangles = state factors, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships. Numbers next to relationships are keyed to [Table 9](#).

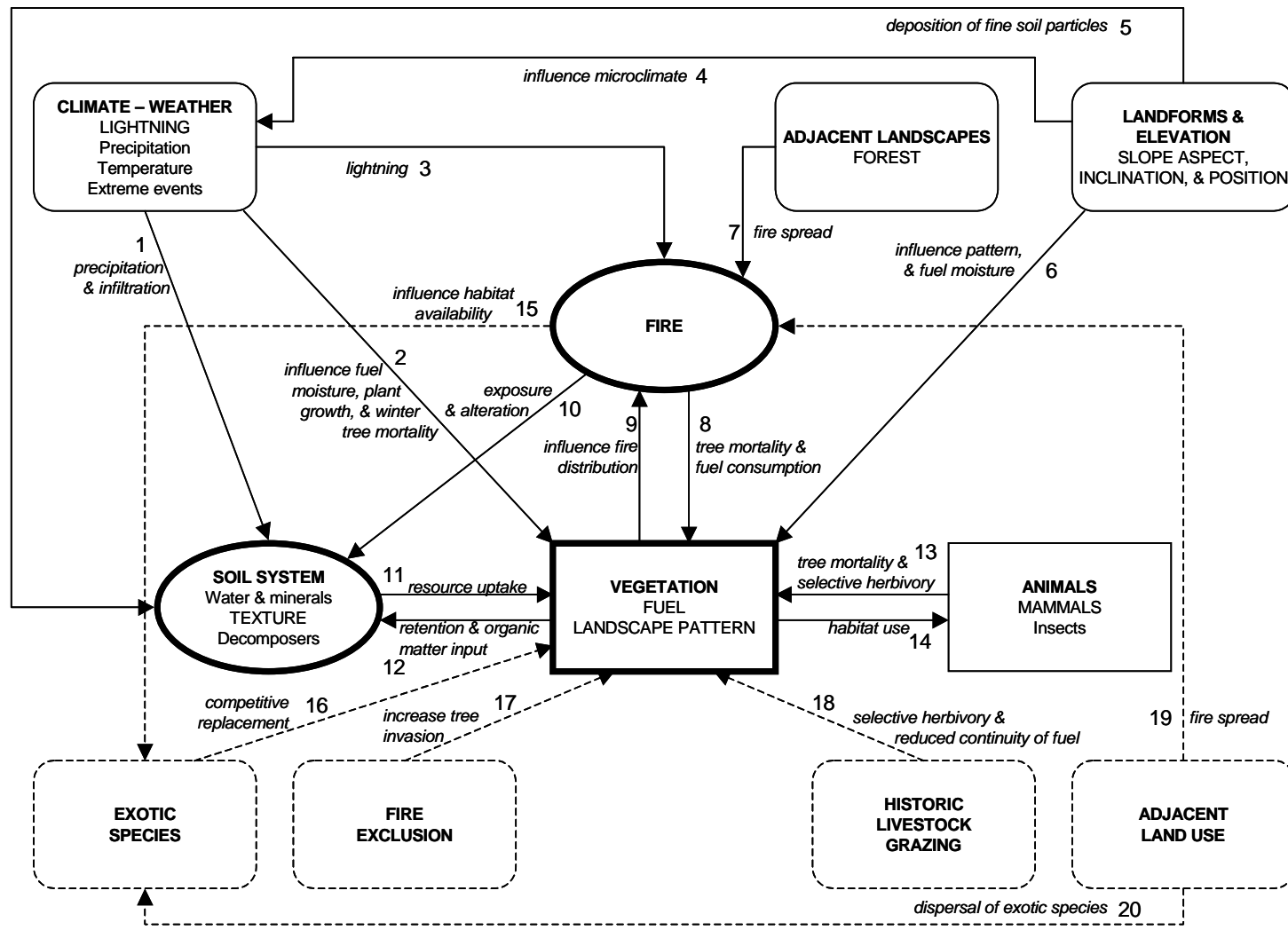


Table 9. Explanation of relationships shown in ecosystem characterization model of Montane-Subalpine Grassland. Numbers for relationships are keyed to [Figure 16](#).

Relationships	Circa 1880	Today
1	Precipitation & infiltration add to soil moisture.	Same.
2	Climate is major factor determining plant growth. In grasslands on slopes, small trees die in winter when water lost in transpiration (driven by intense solar radiation) cannot be replaced by water from frozen soil.	Same.
3	Lightning ignites fires in adjacent forest.	Same.
4	Landforms, especially slope factors, result in microclimate variation.	Same.
5	In grasslands in valley bottoms, slope position results in deposition of fine soil particles within the grassland.	Same.
6	In grasslands on slopes, uniformity of slope leads to homogeneous vegetation pattern. In grasslands in valley bottoms, landform characters influence size and shape of meadows, as well as distribution of species.	Same.
7	Fires spread into ecosystem from adjacent forest ecosystems.	Same.
8	Fires kill above-ground stems of plants, including tree seedlings, and consume fuel.	Same.
9	Homogeneity and continuity of vegetation facilitates spread of fire.	Same.
10	Fires expose soil surface.	Same.
11	Water and minerals in soil are absorbed by plants.	Same.
12	Plants stabilize soil and produce litter.	Same.
13	Herbivores graze vegetation. Unusually high deer populations can reduce the herb layer.	Same.
14	Vegetation serves as habitat for animals.	Same.
15	Not applicable.	Disturbance inside SCPN units creates habitat for exotic species.
16	Not applicable.	Exotic species successfully compete with native species. Some exotics may have the potential to alter ecosystem processes.
17	Not applicable.	Fire exclusion by NPS results in tree invasion.
18	Not applicable.	Historic livestock grazing likely reduced herb cover, changed species composition, and reduced the continuity of vegetation.
19	Not applicable.	Human-caused fires originating outside SCPN units may spread into units.
20	Not applicable.	Disturbances in lands adjacent to SCPN units provide habitat for establishment of exotic species, which are then more likely to be dispersed into the units.

Figure 17. Ecosystem dynamics model of Montane-Subalpine Grassland. This model provides more detail on the vegetation - fire portion of the ecosystem characterization model (Figure 16) by showing the various communities (within different states) and processes that form them. Numbers next to relationships are keyed to Table 10.

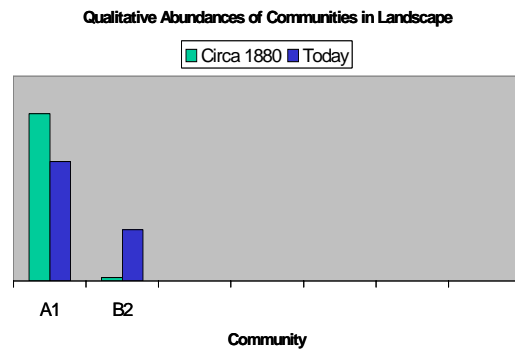
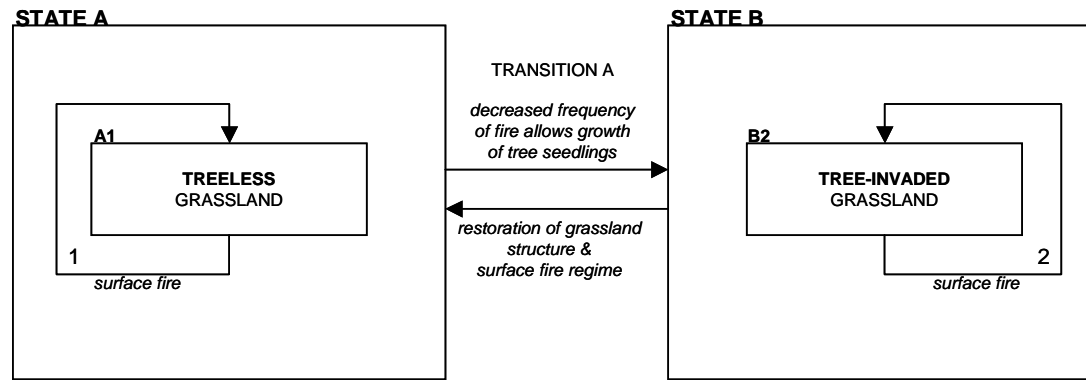
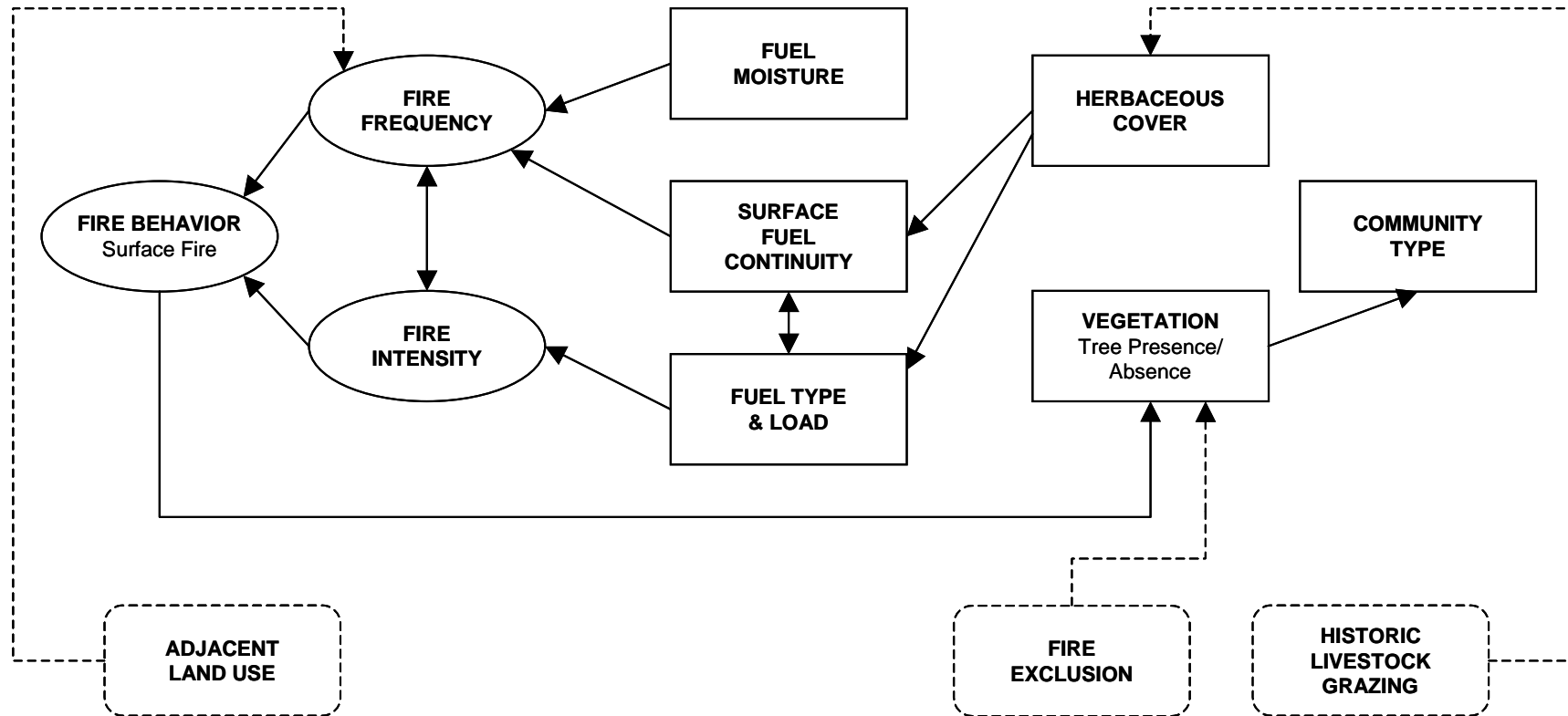


Table 10. Explanation of relationships and transition shown in ecosystem dynamic model of Montane-Subalpine Grassland. Numbers for relationships are keyed to [Figure 17](#).

Relationships and Transition	Circa 1880	Today
1	Post fire stands are regenerated by sprouting.	Same
2	Post fire stands are regenerated by sprouting.	Same
A	Uncommon	Transition from State A to State B occurs as fire exclusion reduces fire frequency and thereby allows establishment and growth of trees. Reversion to State A requires tree cutting and restoration of fire regime.

Figure 18. Mechanistic model of Montane-Subalpine Grassland. This model provides more detail on the mechanisms involved in the vegetation - fuel - fire interaction of the ecosystem dynamics model (Figure 17). Symbols are as follows: rectangles = biotic components, ovals = interactive controls, and dashed rounded rectangles = anthropogenic stressors. Text within symbols includes title (in bold) and important features (key features are in upper case). Lines are as follows: dashed lines = relationships involving anthropogenic stressors and solid lines = other relationships.



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